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THE NUTRITIAL ACTIVITIES OF THE CALIFORNIA WOODPECKER (BALANOSPHYRA FORMISCIVORA)

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INTRODUCTION

THIS paper is a portion of a more comprehensive study on the same general subject. Two objectives are aimed at in the whole study. One is to increase knowledge of the activational side of life in a particular avian species, certain of which activities are sufficiently unusual to elicit a rather unusual degree of popular interest. The other objective is to use the case for calling the attention of zoologists and others to the indubitable fact, as it seems to me, that here is a large and important segment of the phenomena of animal life to which relatively little scientific attention ever has been given or is now being given.

The closely related group of questions arising from the phenomena may be laconically worded thus: To what extent do animals make their heads contribute to their success in life? Stated a little more formally we may say: In exactly what way and in exactly what measure do animals use their heads toward solving the problems by which they are ever confronted in nature and which give rise to man's concept of struggle for existence? "Heads" is here used in no figurative sense—as a certain popular mode of expression might lead one to suppose. It implies the entire anatomical and physiological constitution of this portion of the animal organism. Certain members of the portion, viewed thus, spring naturally into prominence. These are the brain, the eyes and ears, and the mouth.

That the phenomena are not receiving the scientific attention they deserve may be seen by referring to two of the specialized fields of animal biology which would seem peculiarly the ones to which the phenomena should belong. These are *animal ecology* and *comparative psychology*.

Ecology is so recently differentiated within the science of living nature that the word had not yet got a place in the Century Dictionary of twenty-five years ago. Were we to take at its face value almost any definition of ecology, we might suppose it would include such a study as is here reported. For instance, "ecology is that branch of general physiology which deals with the organism as a whole, with its general life processes as distinguished

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from the more special physiology of organs" (Shelford, 1913, p. 32). This is certainly broad enough, and specific enough by implication, to include such a question as ours; yet I find scarcely a hint of any such question in the important book from which this definition is quoted.

The new book by Shelford, Laboratory and Field Ecology (1929), reached me too late to enable me to note statements in this important work that bear significantly on my view of mentality as a factor in animal ecology.

Nor does this type of question fare much if any better in very recent ecological writings. "Ecology is a new name for a very old subject. It simply means scientific natural history." (Elton, 1927, p. 1). Devoted to the ecology of animals as is the excellent book thus drawn upon, one might easily suppose our question would be appropriate to it. Yet apparently the author of the book does not think so. At any rate nothing in its pages indicates that he does. On the whole it seems that by a sort of tacit agreement, possibly on grounds of convenience, phenomena of the kind we are concerned with are excluded from this newly named old subject.

Working animal ecologists perhaps consider that phenomena involving the minds of animals, as our question does, belong properly to psychology and should be left to the special students in that realm. Nor does this seem unreasonable. Yet what has actually happened is that the phenomena are excluded from comparative psychology as this is now studied, and, so it appears, conceived, quite as thoroughly as from ecology. Almost without exception present-day investigators in this science have set as their goal the observation of animals under controlled conditions and so of necessity they have retired to the laboratories. This goal and technique, unquestionably important though they are, and fruitful of results in various ways, yet have no place in their programs of work for the class of phenomena here dealt with.

This definite, formal debarment of studies of this kind from comparative psychology of the modern period is specially well seen in the writings of C. J. Warden (1927 and 1928). But imprimatur itself is less convincing evidence on the point than that which may be gained from inspecting actual publications in the field. The paper I am now writing would be almost as much out of place in any current psychological publication (American at least) as in a botanical or geological publication. Were I to approach the editors of, say, *The Journal of Comparative Psychology* relative to publication, I should be prepared to receive with the adverse decision some such suggestion as that although the facts presented are rather interesting they pertain to geography or natural history, or, more specifically, to ornithology and not to psychology, even though a few of them have an indirect bearing on that science.

But while the phenomena in question do not come within the province of any really modern science (modern science as such science now defines itself) they are by no means neglected altogether. In fact they are receiving a good deal of attention in several countries by what may be called scientific amateurs. A considerable list of very painstaking field observers might be drawn up with mention of their contributions to knowledge of the general sort here treated. The United States and Germany would be well represented in the list; but the British Isles would almost certainly be the most extensively represented.

By way of illustrating from the side of publication what is referred to, I mention *British Birds*, edited by H. F. Witherby. The twenty odd volumes of this scientifically unsponsored journal are a real storehouse of observational facts similar to

those recorded in this essay. The difference between the treatment of them by writers of the class here mentioned and that given them by me is that speaking broadly my standpoint demands that the phenomena be viewed more systematically and comprehensively and in certain aspects more critically than is required by the standpoint of most naturalists. For one thing my general view necessitates a technique of perfect balance (as near that as possible) between the qualitative and quantitative aspect of the phenomena involved.

Toward realizing this ideal on the qualitative side I have used terms that are as objectively and uncontroversially descriptive as can be selected. Words like instinct, intelligence, behavior, intention, thought, and reason, which so easily come into descriptions of animal activities, I have uniformly excluded. This I have done not because of any doubt about the general validity of these words or any prejudice against them, but merely from the wish to avoid raising theoretical questions from which I have wanted this treatment to be free.

On the quantitative side, although great exactness nowhere appears, I trust a certain regard for numbers and measure is recognizable at every turn.

Finally the investigation has been pursued and the results written about with the recognition constantly before me that the type of problem must necessarily be basically the same as that to which the nutritial activities of men give rise, even though men's activities are almost infinitely more complex than the corresponding activities of woodpeckers. Basically, I say, the problems must be of the same type for the unmistakable reason that their most fundamental aspects are the same. Food of some sort is certainly no more nor no less indispensable to men than to woodpeckers. Nor do the essentials of digestion, assimilation, and energy utilization differ fundamentally in the two cases.

Furthermore, the heads of the two animals surely have many activities in common. This is especially true as to the brain and the eyes. It is also true, with very important exceptions, as to the mouth.

Is it not, therefore, fair to suggest that studies of this type ought to hold much the same relation to studies on the activities concerned in the nourishment of man that studies on organs concerned in the nourishment of, let us say, the frog and dog, hold to studies on the organs concerned in the nourishment of man?

THE ACORN STORING OF THE CALIFORNIA WOODPECKER

So exceptional and striking are the operations of the California Woodpecker that they can hardly escape the notice of anybody who spends a little time in localities inhabited by it. This is especially true of its food-storing activities. As a consequence some information about its habit is widespread as well outside of, as in, California and all home countries of this and its subspecies. Many general writings of later years on bird life make some reference to the subject. If, however, one seeks information that is detailed and accurate he finds it to be meager indeed. So it has resulted, as usual in such cases, that various assertions about the matter which are "interesting if true" have gained wide currency. But "interesting if true" carries with it, here as usual, certain rather startling implications. If the assertions strike people as interesting it does not matter greatly whether they are true or not. Take one

assertion that is specially prevalent about the food-storing performances of these woodpeckers.

Acorns, it is perhaps superfluous to say, are by far the most common objects stored. The favorite explanation of this is that what the birds are really after is not the meats of the nuts but the "worms" by which the acorns will become infested after they have been stored for a while. Just why this explanation is so popular is a question more of human than of bird mentality. It does not, therefore, fall within the purpose of this discussion. Enough to say that I have not found a single item of critical evidence in support of it.

On the other hand, the evidence that the meats of the acorns are eaten by the birds abundantly and regularly is ample. The contrary notion seems to have become a sort of folk story and so is nearly beyond the reach of science to correct. Some of the affirmative evidence is, however, significant for the present discussion. The consumption of the meats themselves has been observed by several naturalists, e.g., Bendire ('75), Henshaw ('21), and Ritter ('22); but the real place of the nuts in the birds' food supply could hardly be determined otherwise than by a study of stomach contents. Several such studies have been made, the most important of which are by Beal ('11) and Neff ('28).

From the examination of the contents of 84 stomachs, Beal found 53 per cent of the whole to consist of acorn material. These stomachs represented birds taken in every month of the year except February, April, and May. Twenty-three of the stomachs contained nothing but acorns; and twelve taken in November contained 93 per cent of nuts.

Neff's figures for the 73 stomachs examined by him differ considerably from Beal's, the most striking difference being the 49 per cent of "mineral matter" which he reports. "Acorns," he says, "were the commonest vegetable food, averaging 29 per cent for the year, and were taken more regularly than any other item of food."

The examination of the contents of three stomachs of the California Woodpecker, collected by Mr. W. H. Burt in Tehama County, California, October 30-December 2, 1928, gave the following results expressed in the form used in Food Habits Research, Bureau of Biological Survey, United States Department of Agriculture. The examination was made by E. R. Kalmbach.

1st specimen
Condition of stomach: ¾ full
Percentage of animal matter, 1; of vegetable, 99; of gravel, etc., 30
Contents: Trace of unknown beetle, 1%; Fragments of a *Vespula* sp., 1%
A mass of acorn mast, 99%

2d specimen
Condition of stomach: full
Percentage of animal matter, trace, of vegetable, 100; of gravel, etc., 35
Contents: Jaw of an ant, trace: Acorn mast, 100%

3d specimen
Condition of stomach; full
Percentage of animal matter —; of vegetable, 100; of gravel, etc., 40
Contents: A mass of acorn mast, 100%

For interpreting these figures, it should be said that the quantity of "gravel, etc." mentioned means the portion by volume of the entire mass found in the stomach. E.g. the mass contained in stomach No. 1, was composed 70 per cent food material and 30 per cent "gravel, etc."

The well-nigh exclusive acorn diet of these three individuals is probably correlated with the fact that they were taken at about the height of the acorn season.

Attention should be called to the liberal amount of "gravel, etc." found in the stomachs and also in those examined by Neff. This suggests the possibility of a connection between gravel-eating and pebble-storing, noticed later.

INSECTS IN THE WOODPECKER DIETARY

Beal's formal statement that "larvae are almost entirely wanting" in the stomachs examined by him, "while acorns are eaten freely," is significant in its bearing on the general question of the bird's utilization of insects as food. It confirms the impression one gets from field observations that for the insect component of their dietary they depend less on the typical wood pecker method of digging for grubs than on the fly-catcher method of capture while both prey and themselves are on the wing. And this again

agrees with the great general activity of this as compared with any other woodpecker.

That the several kinds of insects which, in larval and other stages are known to infest the acorns are also frequently eaten by the birds is undoubted. But this is no evidence that the birds do not eat the acorn meats, nor that the insects are the main object of the storing. The bird's food requirements are almost certainly what has led to the storing activity; and whatever in the acorn complex will contribute to that end may properly be said to be explanatory of the activity.

The cursory study I have been able to make, with the help of my entomological colleagues, Professors E. O. Essig and C. W. Woodworth, of the insect population of the acorns shows clearly that this is of itself an interesting problem collateral to the one I am concerned with, but altogether too complex for any but a professional entomologist to handle successfully.

But the fact that the meats of the acorns and not the insect inhabitants of them are the chief utility to the birds must not be taken to imply that acorn meats are eaten to the exclusion of insects. As a matter of fact, insects enter largely into the dietary of the birds. But to a large extent the insects consumed are flying ones caught while in flight. This woodpecker is almost as exceptional among its kind for its fly-catching activities as for its storing activities. Its performances in this connection constitute a subject of study in itself and are outside the scope of this article.

HOW USEFUL IS FOOD STORING?

My interest in the storing phenomenon exhibited by these woodpeckers dates from about 1907 or 1908. Quite casual at first, my attention to it has gradually increased until during the last decade I have devoted all the time to the subject that other more formal duties would permit. The freedom from official obligation of the last two years has enabled me to make rather careful though far from adequate observations on this aspect of the bird's life over most of its range in California. As a consequence I now feel that the problem is pretty well "staked out" in my mind, my notes, and my photographs and so is ready to be followed into its many details. More intensive field work, supplemented at various points by experiments, would undoubtedly bring added light on numerous questions raised and as yet only partly answered.

The aim of this article is to present the facts relevant to the following aspects of the general phenomenon: Assuming that the storing activity has arisen as an adaptation in the more general food-getting activities of the species, (1) What, if any, evidence is there that this unique activity (unique as compared with the food-getting activities of other species of woodpeckers) gives this species special advantage over other species? (2) How effective is the activity when considered in detail and on the supposition of its being fundamentally a special activational adaptation?

THE WOODPECKERS AND THE OAKS

So thoroughly dependent are these woodpeckers on the genus *Quercus* that nothing approaching a full answer to the questions asked is possible apart from a considerable study of this genus of trees throughout the bird's range. This woodpecker is bound to the oaks almost as closely as any species of parasite is bound to its host. But even so there is variety enough within the quercine genus utilized by the avian species to give the woodpecker a good deal of chance for variety in its food-getting activities and in its life generally.

Viewed from the standpoint of the "web of life," now so important a tenet of all biological naturalists, the California woodpecker must be looked upon as the avian species (not merely picidean species) which has surpassed all other avian species in utilizing for food the acorn crop of this particular geographic and arboreal region. In doing so this woodpecker has brought itself into close dependence on the oaks not only for food

but in various other ways, notably in its reproductive affairs. Furthermore, this dependence on the oaks has resulted in dependent relations of the birds with various other species of trees and other objects, as wire-line poles, fence posts, and human habitations.

And finally the bird's quercine association has brought it into special relations, largely competitive, with various other species of animals. Among these competitive animals the California jay (*Aphelocoma californica*), and crested jays (*Cyanocitta stelleri*), and the California Gray Squirrels (*Sciurus griseus*) are specially to be mentioned since they appear to be the chief, though by no means the only, depredators on the stored acorns. These marauder species have to be noticed because security of the stores against them depends to a considerable extent on the way the storing is done (e.g., Ritter, 1921). A comprehensive treatment of the bird's relations with other animal species resulting from its storing activities would have to include a consideration of the uses to which men have put the acorn crop. For instance that these nuts were a chief element in the food supply of many of the California Indians is well known. And acorns have been and are a considerable factor in the hog, sheep, and turkey industries of California. Here as everywhere the web of life, if followed far enough, turns out to include man in one way or another more often than otherwise in some very practical way. But this aspect of the general problem outstrips the aims of this study.

GROGRAPHICAL DISTRIBUTION OF THE CALIFORNIA WOODPECKER

So fundamental is the relation of the California woodpecker to the oaks that the suggestion naturally comes of a map of the region to show the distribution of these trees. But such a map would not be of much value as an aid to the present discussion unless it contained various details that are only partially worked out in the field, and are not yet reduced to map form. The details referred to concern various facts of ecological association, some of the most important of which for this study are too local to be cartographically represented except on maps of large scale. The following brief general statements aided by a very general map, figure 9, will serve the present needs. By a rough estimation, based on data contained in *The Silva of California*, by W. L. Jepson, on Jepson's personal help, and on my own field work something less than 50 per cent of the area of California may be counted as occupied by species of oaks and consequently as being the habitat of the California woodpecker. This gives the species approximately 70,000 square miles of territory within the limits of this State. And this nearly covers the case, since the species extends beyond these limits only to a short distance northward, into Oregon, and southward into Lower California.

The acorn-storing woodpeckers of Lower California have recently (J. Grinnell and H. S. Swarth, *The Condor*, Vol. 28, July, 1926, pp. 176–178) been recognized as two subspecies, *Balanosphyra f. martirensis* (northern part of the peninsula), and *B. f. angustifrons* (south end of the peninsula). Although these birds are storers, the fact that they present slightly diminished head sizes, especially in the beak, as compared with the Californians proper, suggests differences of some sort in the storing habits. But I know of no observations to prove this; and my own studies have not extended into this territory.

The north-south range of the California woodpecker is thus something more than a thousand miles. Altitudinally its range is from the sea coast to elevations of 4,000, 5,000, and even 5,500 feet. These ranges in latitude and elevation imply several different arboreal asso-

ciations, some of which differ sharply as affecting the requirements of the woodpeckers. This point will figure in portions of this discussion.

Coupled with this exceptionally varied range of the species is the fact of its slight migratoriness. Typically the birds are segregated into groups of larger or smaller numbers, the locations of these being determined by the more or less sharply group-wise distribution of the oaks. This distribution of the oaks is in turn largely dependent on the precipitation and stream courses. There is very little in California corresponding to the oak forests of more humid regions.

These groups, some of them particularly, are remarkably constant in numbers and areal boundaries. Year after year, decade after decade, and probably century after century they remain much the same. The question of how much intercourse and interchange there is among them is important but we have almost no information on it.

ADVANTAGES OF THE STORING HABIT

Now we turn to the first of our formal questions, namely that of the special advantages, if any, that accrue to the birds, from the storing habit. There are two outstanding facts concerning the species which are closely correlated with this habit, and may justifiably be interpreted as benefits resulting largely from the habit. One of these facts is that the groups may flourish in localities which constitute remarkably different environments as compared with the environments surrounding most woodpeckers.

To illustrate, compare the set of conditions surrounding the two groups designated in my notes as the Ojai group and as the Palomar group. These are both exceptionally and about equally populous and flourishing. The Ojai group is in the small Ojai Valley, about 50 miles from the coast at Ventura, its elevation being 900 feet. The temperature here ranges from a maximum of 119°F. to a minimum of 13°F. with a mean of 61°F. The mean annual precipitation is about 24 inches, this being all rain and confined almost entirely to the winter half of the year. The oaks here are the Valley oak (*Quercus lobata*) and the Coast Live oak (*Q. agrifolia*). There are few trees of other species. The shrub and annual vegetation is also of moderate development. The Valley has been intensely agricultural and horticultural for nearly or quite a half century.

The Palomar group is well toward the southern end of the state in San Diego County on top of a long, broad mountain, the group's elevation being about 5,500 feet. The summer-winter range of temperature is from 100°F. to 9°F. with a mean of about 64°F. The region has a mean rainfall of 50 inches, most of which is winter rain, though rains in late summer are frequent. Heavy winter snows and drenching fogs are common. The prevailing oak is the Black oak (*Q. Kelloggii*) but the Maul oak (*Q. chrysolepis*) is common, its acorns being, secondarily to those of the Black oak, an element in the food supply of the birds. Several species of conifers come into the arboreal association, the most important of which from the woodpecker standpoint are the White fir (*Abies concolor*) and the Incense cedar (*Libocedrus decurrens*). Furthermore, the shrub and annual plant vegetation is varied in kind and luxuriant in growth for California.

It will thus be seen that in these two localities, we have to do with environmental conditions the differences in which would hardly be greater for equal areas of the United States bordering the Gulf of Mexico to the south, and the Great Lakes to the north. Yet as already said, populations of this woodpecker flourish the whole year through and year after year in these localities. Several other equally contrasted pairs of groups have come under my observation, for instance in the Visalia district of the San Joaquin Valley, elevation 334 ft. and the Yosemite Valley of the Sierra Nevada Range, elevation about 4000 feet. Also a colony in Mendocino County of northern California, and a seaside colony in Santa Barbara County 650 miles away in southern California.

While I would not attribute the species' unusual adaptiveness as thus exhibited to its storing habit alone it appears certain that to it and its correlated habits the adaptive phenomenon is largely due. It would take us beyond the purposes of this article to go into this matter fully; but one item is so relevant to the point that it must be noticed.

WOODPECKER SOCIOLOGY

Heretofore, we have spoken of the groups of individuals into which this species is so largely segregated, and have referred to the sharp localization of many of these. Looking more closely we find conditions which justify our speaking of the groups as settlements presenting some of the characteristics and advantages which appertain to settled as contrasted with nomadic human populations. Indeed the resemblances between these settlements of California woodpeckers and those of the California Indians are so unmistakable that the familiar name *rancheria* applied to the Indian settlements since the Mexican-Spanish period of California readily suggests itself. For some years I have recognized that to follow out in detail the social aspect of these woodpecker settlements is almost the major problem presented by the natural history of the species. But an execution of such a task will require much more extensive studies on various activational and structural phases in the lives of individual birds than have yet been made.

I would not give the impression that the distributional facies as one may say of the entire species, presents nothing else than these settlements. The truth is, a goodly number of individuals in many localities are seen where nothing of the settlement idea is recognizable. Rarely, however, according to my experience, does an individual occur quite alone. Whenever one is seen or heard, at least one other, usually more, may be expected. It is largely a question of oaks. Almost anywhere in California where there is a considerable assemblage of oaks if many of the trees are large a settlement of the California woodpecker is to be looked for. The size of the trees is an almost constant factor in the situation. Map the distribution of large oaks in the state and you map very nearly the settlements of these birds.

But there are very considerable areas of oaks of small and medium size. This is especially true of the Coast Live oak in parts of the coast ranges of mountains; and of the blue oak (*Q. Douglasii*) of the lower foothill belt of the Sierra Nevada. It is in these areas that the scattered or diffuse element of the population chiefly occurs. What the relation is between the scattered and the settled population is not at all well known.

RESIDENTIAL HOLES

In almost all cases the trees which furnish the birds with acorns and those used for storage are likewise the residences of the birds. This is especially so when, as often happens, the same tree both yields the acorns and serves as a granary for them. In other words relatively safe and permanent dwelling-places and relatively ample and ready-at-hand food supplies are in close proximity, not merely for a short breeding period, but throughout the year, and year after year.

Concerning what such interlocking of needs and activities means for animal life generally, we know a good deal, but not enough. Particularly are we poor in observational knowledge of such needs and activities during the incipient stages of highly complex modes of life and social organization.

In the case of this woodpecker we have some, though inadequate, observations on

the breeding activities. But with these we are not now primarily concerned. The question that does concern us is whether and to what extent the birds use holes made by themselves as places of refuge against storms, cold, animal enemies and so forth.

Although observations under this head are few such as we have are to the point. They show conclusively that the holes are thus used more or less. The most definite published statements on the subject I have found are by Wheelock (1904) and Grinnell and Storer (1924). The former tells us that the birds "return to the same nest tree year after year, but usally excavate a new cavity, frequently utilizing the old as a shelter for the male on stormy nights." (p. 378). While this statement lacks particularity in several respects, the author's experience as a field observer makes it weighty as far as it goes. Referring to certain nest holes under their observation, Grinnell and Storer say: "Individual birds used these for roosting places at night in December, 1914, only one bird occupying each hole." (p. 341).

Mr. Frank A. Leach, though not considering himself a professional naturalist, has long been interested in various aspects of natural history. The grounds of the Mount Diablo Country Club, where Mr. Leach has resided for years, contain one of the finest groves of Valley and Live oaks in the Contra Costa region. This implies a large, flourishing settlement of California woodpeckers.

Mr. Leach has accumulated a large fund of information about the birds. Bearing on the point before us, he writes: "I have frequently seen as many as eight or ten woodpeckers retire in one nest-hole as the dusk of evening marked the closing of the day. Some of these abiding places are used year after year." (Leach, 1925). From correspondence Mr. Leach has furnished me more details about the matter.

Valuable information under this head is due to Mr. C. W. Michael, who for some years has been the postmaster of the Yosemite Valley. Both he and Mrs. Michael are experienced field observers. One of the fruits of their observations on the California woodpecker is quoted from a letter by Mr. Michael of January 12, 1929.

> In reply to your query of January 10, I can say that the California woodpecker does use the nest-hole, or a hole especially drilled for the purpose, as a sleeping chamber and as a place of refuge during storms. I have seen two birds come out of a sleeping hole in the morning and I presumed that they had spent the night together in the same hole. You know that the California Woodpeckers are not particularly early risers. Three birds had a nest-hole in the oak at my door and on more than one occasion I was down stairs early to watch the birds come forth. The three birds, two males and a female, were apparently equally involved in this nest and I was trying to learn if all three slept together. I did not settle the problem as never more than two birds were seen to leave the nest in the morning, but during the day all three birds were seen to go in and out of the nest hole.
>
> Often in the late fall a California woodpecker has been found at work drilling a hole. Now certainly he is not drilling a nest-hole at this time of year. Probably the bird is young and is making ready to spend his first winter.
>
> Up the road a ways there lived a pair of woodpeckers: we called them the "wealthy Melanerpes" because they were the pair that had the vast store of acorns in the bark of two great yellow pines. Their sleeping chambers were about sixty feet above the ground. Each bird had its own hole; the holes were about two feet apart, one above the other. These holes caught the first of the morning sunlight and often on cold mornings when we passed the birds were poking their heads out of the holes and chatting to one another. On rainy days too these woodpeckers were usually to be found looking from their doorways.
>
> In the dead limb which overhung one of the walks in the Valley three woodpeckers had a nest. When the young had flown the limb, which was considered as a menace to the public, was taken down. Immediately the woodpeckers set to work and drilled two new holes a little lower down in the remaining stub. These new holes were used as winter sleeping quarters.

That some other species of woodpeckers use nest and perhaps other holes as places of refuge is well known. Mr. Michael states that the Hairy, the Willow, the Lewis, and the Flicker do so. But in none of these species is there any such permanent and ample supply of food right at or near the places of refuge. The combination of advantages with which the California woodpecker has provided itself is what makes its case exceptional.

It is certain, then, that the holes into which the birds enter are not exclusively nesting places. They are also residential places of more or less permanence. And to some extent holes appear to be made for residences and not merely for breeding purposes.

Another thing about the holes may have a bearing on their efficiency as places of refuge. This concerns their position on the trees. Numerous references are made to nest holes in stubs of dead trees, wireline poles and the like. This implies that such holes are on bare, exposed, upright surfaces. Undoubtedly holes thus located are not uncommon. I have seen such myself. However, I am quite sure these are not the most usual locations.

Quoting again from Wheelock:

> The hole is placed "usually on the under side of a large branch at some distance from the trunk." Several observers confirm this, and it accords with my own experience. So far is it the rule where the woodpecker settlements are most flourishing, that I have come to expect nest holes thus located, and rarely is my expectation amiss. Particularly is this the case where the Valley oak (*Q. lobata*) is exclusively concerned as in many parts of the San Joaquin and Sacramento Valleys; or where the Live oaks (*Q. agrifolia* and *Q. Wislizenii*) are almost exclusively concerned, as in some places, e.g. the sea-side Hope ranch at Santa Barbara; or, finally, where Valley and Live oaks intermingle, as in various parts of the Contra Costa, Santa Clara and Napa valleys. Nor are the nest holes restricted to decaying or even dead parts of the tree. Often they are in limbs or inclined portions of main stems that are alive, and, seen from the ground below, appear quite "sound."

When the tree association consists of the Black oak (*Q. Kelloggii*) and the Yellow pine (*Pinus ponderosa*), or the Incense cedar (*Libocedrus decurrens*), or the Silver fir (*Abies concolor*), so that the trees used for storing are other than those which furnish the acorns, the residential holes are less closely confined to the oaks and less likely to be on the under side of limbs. That residential holes situated on the under sides of large limbs or inclined trunks are specially well located for protection against storms is obvious.

It seems, then, justifiable to conclude that the relatively settled mode of life of these woodpeckers, dependent primarily on their food supply, has contributed importantly to enabling them to flourish about equally well over a geographic and ecologic range that is exceptional if not unique. This we have been stating in the specific terminology of ecologic associations.

We may now state it in the terms of life zones. Of two settlements about equally populous and vigorous, so far as I can see after having observed them rather attentively, one is at Visalia in the lower Sonoran zone while the other is on the floor of the Yosemite Valley in the transition zone.

SIZE OF POPULATION AS MEASURE OF SUCCESS IN ADAPTATION

The second fact I take as evidence of special usefulness of the storing activity is the abundance of individuals of the species, as compared with any other species which inhabits the same area either as a whole or as any "ecologic niches" within that area. It should not be forgotten that in almost any geographic area as large as that occupied by this woodpecker, local differences occur which on the one hand are unsuited to the species concerned, and on the other hand are

suitable for other even closely related species. This is especially true in an area so topographically and latitudinally varied as is the state of California. It is partly this sort of thing that has led to the conception of ecologic areas or "niches" e.g. Grinnell (1914, p. 91) for general discussion and illustrations of this conception.

Seven other species are entitled to consideration under this head: The Red-shafted flicker (*Calaptes cafer collaris*); the Lewis woodpecker (*Asyndesmus lewisi*); the Downy woodpecker group (*Dryobates pubescens*); the Nuttall woodpecker (*Dryobates nuttallii*); the Hairy woodpecker group (*Dryobates villosus*); the Red-breasted sapsuckers (*Sphyrapicus varius*); and the white-headed woodpecker (*Xenopicus albolarvatus*).

In not many aspects of zoology is there greater lack of reliable quantitative information where such information is important than in that of numbers of population. This lack is largely due to the difficulty of census taking for most kinds of animals. The difficulties are surely real and in many cases well-nigh insurmountable. However in my opinion this difficulty is not alone responsible for our meager knowledge under this head. A perhaps equally influential factor has been an insufficient urge from recognition of the bearing of this problem on other still larger problems. For instance, in cases in which the number of individuals of a species or some regional segment of a species is seen to be important from the hunter's or nature lover's standpoint census-taking studies have been made with considerable success.

So far as I am aware zoologists have given little attention to number of population as a criterion of the relative success of kindred species and hence as measuring the degree of their adaptation. Particularly has the matter been neglected insofar as success depends on the activities, as contrasted with the structure, of individuals. The prevalent conception has been that the numbers of each and every species are controlled by the available food supply. All species are practically unlimited in reproductive capacity and hence are always crowding their means of sustentation whether this be plentiful or scant. Given times or places of great abundance and up go the numbers to meet it. Per contra, given times or places of great scarcity and down go the numbers correspondingly. This is held to be the "law" for any species just as much as for any other species.

THE ACTIVITIES OF ANIMALS AS A FACTOR IN THEIR WELL BEING

The question of whether the way each particular species has of utilizing its sustentative resources cuts any figure in situations as actually presented appears to enter exceedingly little into the problem as zoologists have conceived it. Inevitably, however, if one approaches the general phenomenon of animal life with his view fixed chiefly on the total round of individual activities he can not avoid the queries, What exactly are these activities? What do they count for toward the well being of their performers?

These queries as applied to one set of the activities (the nutritional) of one species are central in the present study. Unmistakably the storing activity of the California woodpecker involves nothing so deviative from the general woodpecker type of action as to call out much if any structural modification. The bird merely uses its mechanism to somewhat different immediate ends from those to which its kindred use theirs. Consequently no inquiry is closer to our starting point than that of whether the modified use to which

the bird puts its mechanism gives it any advantage over its kindred in their common struggle for life. And surely one test of the matter must be that of whether, assuming them all to be on an equal footing in inherent reproductive ability, our bird outdoes its kindred in bringing its individuals through the full cycle of their lives.

THE RELATIVE ABUNDANCE OF WOODPECKERS

No effort has ever been made so far as I know to estimate the total number of Californian or any other species of woodpecker. Nor have I attempted the task. What I have tried, as an initial step toward better efforts in this direction, is to estimate the relative abundance of the several species in the geographic area which includes the species with which I am primarily concerned. While I make no pretense of having approached numerical exactness, the results justify, I am confident, the assertion that the numbers of this species distinctly exceed the numbers of its two nearest competitive species, and exceed by many times the numbers of the five other species listed above as belonging to the geographic area of the California woodpecker.

A few words must be spoken about certain liabilities to error due to peculiar conditions under which the numerical estimates have to be made. One of these is the fact that the tree associations favorable for this woodpecker are particularly favorable for human habitation. This brings it to pass that birds and men are thrown together by nature's arrangements more obtrusively than in the case of any other woodpecker, even if not more than in the case of any other native bird except the House Finch (*Carpodacus mexicanus*). Over and over again in many parts of California larger or smaller villages, country homes of city dwellers, golf courses, and farm residences are located as they are because of the fine development of Valley or Live or Black oaks. And these are exactly the places most favorable for settlements of this woodpecker. Among the most prized occupants of many a California door-yard are a few or several splendid oaks. So it happens that thousands of people in the State are more or less familiar with these birds, not from any special effort, but because environic conditions force it on their attention. It is this that credits the bird with being the most "sociable" of all our woodpeckers.

Add to this tendency to natural juxtaposition of humans and woodpeckers, the bird's unique food habits, its noisiness, its striking color displays and its open air flight, and we have a combination of circumstances favorable for recognizing and so for estimating numbers of individuals that does not hold for any other species. Numerical estimates must make due allowance for these encouragements to error.

My presentation may begin with the information from observations other than my own. A questionnaire seeking data on various aspects of the birds' activities was sent to a number of members of the Cooper Ornithological Club selected with reference to their residential distribution in the woodpecker's geographical area. Of the two questions designed to gain information about population, one asked for the species of woodpeckers occurring in the informer's locality. The other was, "What do you judge to be the order of abundance of these species?" All who answered were persons considerably experienced in observing birds, several of them highly accomplished in this way. There were eighteen answers to these two questions. Fifteen of these gave the California woodpecker first rank. The other three gave this place to the red-shafted flicker (*Colaptes cafer* subsp.). Furthermore, the flicker was assigned second place by five persons and the Lewis woodpecker (*Asyndesmus lewisi*) by one person. These estimates correspond pretty well with those derived from conversation with some of the best of our local ornithologists. That the flicker is next most numerous in the area as a whole seems probable from the available data. However, in the opinion of Dr. H. C. Bryant, one of the most

widely experienced of California field zoologists, the flicker outranks the California woodpecker in the area.

But the assignment of first rank to the flicker by three of my questionnaire informants does not so much imply a general disagreement with the others as a difference of abundance dependent on localities. To those who have given any attention to woodpecker life, the statement is hardly necessary that although flickers are genuine woodpeckers in most of their structures and activities, in certain respects they are quite apart from their ordinal kind. So largely is their food obtained from the ground, notably from ants and other ground-inhabiting insects, and so little from trees, that their ecologic niche is quite different from that of other woodpeckers. To make an interesting story short, while the California woodpecker is mainly restricted, because of its food and food-habits, to certain ecologic areas within its geographic area, the flicker is able, because of its food and food-habits, to live not only in the same sub-areas occupied by the California, but in many other sub-areas where the California cannot live. Wherever nesting places are available, this typically implying trees, there flickers can and do thrive.

The only other possible claimant to populational equality with the California woodpecker is the Lewis. In some localities at some times this species far outnumbers the California, e.g. Bryant (1912). And since acorns are eaten by it to a significant extent, it becomes a sharer so far with the California in the latter's ecologic niche. But the Lewis is sharply different from the California in its general nutritional and correlated activities. Indeed as thus viewed the two species are nearly the antithesis of each other. While the California represents the acme of settled life and social intercourse in the order of woodpeckers, the Lewis represents the roving, individualistic life at almost its climax. If therefore the success of the picidean species inhabiting this part of the world is partly measurable by number of individuals, the three species here noticed would be entitled to the highest rank with, however, the California woodpecker distinctly in the lead.

This statement marks off at once activity problems for these other two species comparable with the problem under treatment for the California. But we can do nothing with them here.

A WOODPECKER CENSUS

I now present my own populational studies.

Since both sight and sound are essential modes of observation in field work of this kind: and since it is not always possible to be sure that an individual heard is another than one seen, it is often important that the mode of identification should appear in the record. My record of a trip to the Diablo Country Club, February 8, 1928, will be used as a sort of measuring-stick for the records in general. The observations entering into this record are particularly useful in this way because exceptionally fortunate in having been made by two observers (Mr. Frank A. Leach and myself) and in the number of species observed at the same station during the same brief period.

The record stands: California woodpecker, twenty-five at least (seen or heard). Flickers, four or five (seen or heard). Red-breasted sapsucker, one (seen). Nuttall woodpecker, one (seen). This numerical standard for the California woodpecker will refer more to density of population than to actual numbers, and will be on the basis of the number here esti-

mated (25) in approximately an hour's observing over approximately a square mile of area.

Before considering the mass of records a brief statement is necessary about the way the field-work is carried on. The aim is to cover as much as possible of the geographic area of the California woodpecker. This implies that considerable of the territory traveled must be through places where the birds do not occur at all, or only sparsely or sporadically. This will be readily appreciated from what has been said about the dependence of the birds on oaks, and the character of the distribution of these trees. Travel is by automobile. As I am seated with the driver, who handles the vehicle with sole reference to the work in hand, stops and little off-the-road trips are readily made in response to what the constant look-out suggests. By this means many stops are made for examining localities where either the birds are obviously present or the general conditions are favorable for them. But stops are by no means alone in yielding information.

Birds and their work are often seen and entered into the notes without the automobile's coming to a standstill. From this mode of operation it results that two sorts of stations may be conveniently recognized: namely, those at which considerable time (from an hour to a day or more) is devoted to the observations; and those at which some though not much (less than an hour) of time is spent. These two kinds of station may be designated as "defined" and "undefined." Working in this way brings it to pass that a presentation of the data in tabular form is not profitably possible in the present stage of the investigation.

The records of a round trip of 800 miles through the interior valleys of the Coast Range of Mountains to Humboldt Bay north of San Francisco Bay, August 3–11, 1927, will be examined first. This set of records contains fifteen defined stations. At the three northern-most stations located well within the country of the Coast Redwoods (*Sequoia sempervirens*), no California woodpeckers were found; and from resident observers of birds the information was gained that the species does not occur here. The most abundant woodpeckers, according to these observers, are the Hairy and the Downy. The Flicker is common and the Red-breasted sapsucker not rare.

At all but one of the twelve other stations the records show the presence of the California. But at only three was the abundance comparable with the Diablo standard. At one of these three, that near Willits, there is a settlement almost on a par in numbers and thrift with the Diablo settlement. The favoring tree association here is of the Black oak-Yellow pine type. No other woodpeckers were observed. Another of the three stations just referred to is at Vichy Springs. Though the woodpecker settlement here is distinctly less populous than the Diablo settlement it seems to be well established and flourishing. Four Californias were seen at one time on the same tree, and certainly a goodly number of others were in the vicinity. One Flicker was heard and, doubtfully, one of some other species (Hairy?) was seen. The dominant tree association is the Black oak and Oregon Oak (*Q. Garryana*) and the Digger pine (*Pinus Sabiniana*).

The last of this group of three stations was in the vicinity of Lakeport on Clear Lake. This is primarily a locality of Valley oaks in association to some extent with the Common Cottonwood (*Populus Fremontii*). The presence of Cottonwoods I note particularly, as these trees are here used for both storing and nesting, which is rather exceptional. Although the number of Californias was considerable it seemed to fall distinctly short of the Diablo standard. No other woodpeckers were observed. None of the other nine records of this series show numbers or associative conditions which justify using the term settlement in connection with them. From one to a few—two or three—individuals were observed. No other woodpeckers are mentioned as having been observed directly; but the work of sapsuckers, in no instance fresh, was noticed at several stations.

A concluding statement certainly well within the bounds of the data is that although in the territory covered by this trip the numerical ratio of California woodpeckers to Flickers is distinctly less than that of the Diablo standard (about 5 to 1) the preponderance of the former over the latter is not in doubt.

WOODPECKERS IN THE SACRAMENTO VALLEY

The group of records next to be analyzed pertains to a round trip of 440 miles through the Sacramento valley to Red Bluff, at the northern portal to the valley. This trip was taken October 28 to November 1, 1928. It had the advantage of two observers instead of one, the second being Mr. W. H. Burt, an assistant and graduate student in the University of California. Mr. Burt's thesis work on the anatomy of woodpeckers makes him an especially valuable helper.

Eight defined stations and many undefined ones figure in these records. A general statement of importance that can be made is that in the northern, or Red Bluff, part of the territory, the Flicker was almost if not quite as abundant as the California; and

that the Lewis was not far behind the Flicker. This estimate agrees with that made by Dr. Joseph Grinnell and Dr. J. Linsdale who did field work over much the same territory in January, 1929.

The considerable stretches of the Blue Oak (*Q. Douglasii*) in this region, consisting of trees that are scattered and not large, are not very favorable for the California woodpecker. The only approach in such places to the settlement form of life of the birds is in the rather few localities where the Digger pine is associated with the oak.

At four of the eight stations there are settlements comparable to the Diablo standard in seeming permanence and activity, and somewhat comparable to that standard in density of population if not in total numbers. These stations are at Joyland near Red Bluff, Orlando, Woodland, and Benali, all north of Sacramento, the last only a few miles away. At two of these, Orlando and Benali, Flickers were in evidence, five or six seen at one time at Benali. The Orlando station deserves special mention from being narrowly limited by its dependence on a tree association which in turn is narrowly limited by a flat-land river course—in this case Stony Creek, a branch of the Sacramento river. The association is of Valley oaks and Common Cottonwoods. There are many settlements in this type of locality in California. They are specially interesting from being favorable for the study not only of the population problem but several other problems connected with the social life of the birds.

Besides the California, the Flicker, and the Lewis, which figure largely in this set of records, the Nuttall and Willow Woodpecker come quite prominently into the picture. The Nuttall is specially to be mentioned, a total of at least a half dozen having been observed. The records of the Lewis, the Nuttall, and the Willow belong almost entirely to the numerous undefined stations. At the stations of this class, the general statement to be made is that so far as they are concerned, the California, the Flicker, and the Lewis were so nearly on a par as to numbers that it would be unjustifiable to say either surpassed the others. But at the four stations mentioned as having settlements of the Californias, their numbers undoubtedly surpassed the numbers of any other species. For this set of records, then, the conclusion is that the California surpasses though not greatly, its nearest competitors, the Flicker and the Lewis.

WOODPECKERS IN THE YOSEMITE VALLEY

The records of a trip to the Yosemite Valley, November 30—December 2, 1928, will next receive attention. Populationally viewed this trip was specially significant in two items. First it afforded a good chance at the question of numbers in the Valley itself. Second, it gave an opportunity for special attention to the woodpeckers of the Blue oak belt of the Sierra foot hills. The trip had again the advantage of Mr. Burt's ability as a field observer.

Personally, I devoted most of my time in the Valley to the woodpecker settlement connected with the grove of splendid Black oaks extending from the Plaza to the Yosemite Lodge. The birds were very active, though little storing was going on. The difficulties of census-taking in these settlements were impressive. The question of how many times the same individuals are being counted, hustling from tree to tree as they usually are, if visible at all, is surely a difficult one. Allowance being made for this and other difficulties, I can not doubt that I observed, either by eyes or ears, twenty-five individuals during a two-hour watch in one small area.

As to numbers in the entire Valley I have no basis for judging beyond the facts that the birds are certainly present in various other places, but generally less numerous than in this place.

As to other species: A few Flickers—hardly a half dozen—were seen or heard. Burt saw one Nuttall and, doubtfully, one Downy. Although the Lewis, the Whitehead, and the Pileolated were present in the Valley at the time, according to Mr. Michael, we looked in vain for them.

Concerning Californias in the Blue oak zone, this trip enables us to assert that they occur through the whole width of it from the upper part in the Blue oak—Interior Live oak—Digger pine association, to the lower part where the oaks alone abound. According to the evidence obtained, the birds are considerably more abundant in the upper than in the lower part of the zone. Much storing in the pines was observed and a considerable number of birds were seen or heard. The low foot hill sub-zone, having oaks only, furnished considerable evidence of storing, particularly in dead trees and in fence posts, though no birds were seen—probably because of the brief stops made. No woodpeckers of other species were observed in the zone. A good opportunity, however, was found for examining some extensive recent work of the Red-breasted sapsucker.

WOODPECKERS IN SOUTHERN CALIFORNIA

By far the most extensive single piece of field work contributing to this study was made in June, 1928. This involved 2000 miles of travel, extending southward nearly to the Mexican boundary. It reached the middle elevation of the Sierra range at the Yosemite Valley and the Giant Forest. It crossed

the Tehachapi mountains at Tejon Pass; reached the middle slope of San Jacinto mountain; the upper elevations of Cuyamaca and Palomar; and extended through the valleys and passes of the Coast Ranges from the Sierra Madre mountains to San Francisco Bay. My field notes include 37 defined stations and a large though uncertain number of undefined stations. It is consequently obvious that a detailed examination of all these records would be a formidable consumer of time and space.

Fortunately, the character of the material is such that we can extract the essence of it with even less attention to details than was given the records of the Eureka trip for instance. What makes such a treatment possible is the fact that in this total of records the California woodpecker overtops all other species in numbers to such an extent as to render a detailed presentation quite unnecessary.

I will speak first of the results as they concern species which are to some degree numerical competitors of the California, namely, the Flicker, the Lewis, the Hairy and the Downy. The numbers of these appearing in the records are so small as to arouse suspicion that there is something wrong. Was the observing or the recording badly done? Or, perhaps, was the country traveled specially unfavorable for all woodpeckers except the California? Or, again, was the scarcity of other species due to the time of year? My greater interest in, and familiarity with, the California than with other woodpeckers may have played some part in the results—as may the country traversed and, possibly, the season.

Whatever the explanation here are the facts: A half dozen Flickers figure in the records occurring at five widely separated stations. Two were seen at one station; one at each of two stations; and one was heard at still another station. At a fifth station the birds were surely present, whether one or two or, possibly, more, I could not be certain as they were in and out of their holes. A single Lewis only was seen with certainty, though probably one other at another station was seen in flight. One pair of nesting Hairys was definitely located. The single Downy seen was the result of a rather extensive search in several places especially favorable for it. Three nesting pairs of Whiteheads were located, two at one station and one at another. Much work mostly old, of sapsuckers and, presumably, of Hairy woodpeckers was examined in many localities. But owing to the uncertainty which prevails among ornithologists as to the identification of these species by their work it would be profitless to dwell on these observations.

These factual statements concerning the numbers of other species may serve to show that at least I had this aspect of the population problem in mind and was on the lookout for comparative data.

We now examine this set of records more inclusively. The tabular form of presentation is possible here.

TABLE 1

Numerical results for California Woodpecker for 37 defined stations, field work of June, 1928, estimates referred to Diablo standard

Greater than standard	2
Approximately same as standard	5
Somewhat below standard	9
Much below standard	9
None observed	12
	37

More notice must now be taken of the fact that the "Diablo Standard" refers to density of population more than to actual numbers. The significance of this distinction is important. The point is well illustrated by the Diablo settlement itself. The numerical data entering into the standard are far from presenting the whole truth for this settlement. To illustrate. During the summer before (1927) that on which the standard was established, the Californias became destructive to the almond crop of a nearby orchard. As a consequence the owner of the orchard trained his shot gun on the offenders. Replying to Mr. Leach's inquiry about the number killed, the orchardist said that he kept no record but there were between one and two hundred of them. This orchard was not troubled by the birds the next summer, 1928, though the crop of nuts was fair. Accordingly none were killed by the orchardist. However between fifty and a hundred "in all probability" were killed in 1928 in the door-yard of a residence not far from the orchard. These were shot for amusement apparently, by the invalid occupant of the place, who was able to sit out-of-doors. In view, then, of the abundance of the birds at this place after such slaughter it seems necessary to suppose that normally the settlement here contains several hundred individuals.

Returning to Table 1, it will be noticed that two settlements are estimated as surpassing the Diablo standard. These are the ones at Ojai and on Palomar. The Ojai settlement, to which I devoted several hours divided between an afternoon of one day and a forenoon of the next, gave me the impression of easily surpassing any other I have ever seen in both density of population and total numbers. And as the area

and the number of trees here are probably greater than those at Diablo, I conclude that the Ojai settlement surpasses the Diablo settlement in both. With the aid of Mr. O. E. MacBride, a teacher of science at the Thatcher school, who gives attention to the bird life of the region, I was able to see that in the Ojai settlement there are two rather well-marked subsettlements, one in the village itself, the other, two or three miles outside the village. Applying the Diablo measuring-stick, a total of two hundred individuals for these two subdivisions of the whole settlement seems to me a very conservative estimate.

Reference should be made to the fact that Mr. MacBride reports that a few Flickers occur in the Ojai valley; and that the Lewis comes there occasionally.

The other settlement ranking with the Ojai on the basis of the Diablo standard is the one on Palomar mountain, with which I spent part of an afternoon and the early hours of the following day. This surely equals the standard in density of population, and perhaps also in total numbers. But as I was not able to delimit the area and number of trees here as definitely as at the other two places, I am more chary about venturing any figure for the total population.

Concerning the five settlements appearing in the table as approximating the standard, the estimate has reference to the actual number (25) of the standard and also to density. I feel sure the estimate is more likely to be too low than too high. A list of these may be useful for further studies. They are: In Tajon Pass below Lebec; at Keen Camp on San Jacinto mountain and at Idyllwild on the same mountain; at a tiny place on a branch of the San Luis Rey river known locally as Shady Nook; and that in a small valley near Montecito. Probably the settlement in Yosemite valley and at Eden Dale farm, near San Jose, should be in this list; but preferring to err on the side of conservatism I have placed them with the nine grouped in the table as somewhat below the standard.

As to the remaining 21 stations appearing in the two columns of the table as "much below" the standard and "none observed," a good deal that might be said must be omitted as not important enough to influence the presentation as a whole.

Summarizing now on what this extensive set of records shows, we may say: The ratio of the California woodpecker to its nearest numerical competitor, the Flicker, is approximately the same for the set as that of the Diablo standard, namely five to one.

The conclusion for the whole territory included in the three sets of records here analyzed would be: While the numerical predominance of the California woodpecker over its main competitors, the Flicker and the Lewis, is distinctly less than over its nearest competitor of the Diablo standard, its predominance over these by two or three fold is hardly subject to doubt.

The question may be asked: Were all portions of the territory included in this survey to be examined as closely as were the portions especially favorable for the California woodpecker, might not the populational results be quite different? This is a legitimate question because many localities within the general quercine territory have no oaks at all or only such as are not favorable for these birds, yet do have various other kinds of trees and so are inhabitable by other kinds of woodpeckers. While it seems probable that the conclusions set forth would be altered to some extent by such examination, my belief is that the alteration would not be great and might affect the results in either direction.

ADVANTAGES OF THE ACORN STORING HABIT

At last, then, we are prepared to answer our question as to what if any advantages accrue to the California woodpecker over neighboring species from its nutritial activities. We have tried to show two ways in which it is a gainer. The habit enables the species to flourish equally well over a somewhat wider range of climatic and other environic conditions than can any kindred species with the doubtful exception of the Flicker.

Again, the rate of mortality of the species is believed to be lessened by its mode of solving its food problem. Evidence for this is found in the greater populousness of this than of related species

which appear to be at least the equal of the California in rate of propagation.

A case could undoubtedly be made for the view that the birds are influenced, probably beneficially, in most if not all their life activities. Their sexual and breeding activities are perhaps most notably thus influenced. One of the most striking attributes of the species as observed in the field is the extent and variety of its vocalization. Mention is made of this by nearly all writers. Viewing the "settlements" both analytically, i.e., as to the individuals constituting them and as wholes the question is close at hand: Have we not here phenomena that may justly be regarded as primordially social and cultural in nature? But this question reaches far beyond the bound set for this paper.

HOW EFFICIENT ARE THE WOODPECKERS?

We now pass to the second of our two initial questions: How effective is the activity we are concerned with? But is not the answer given to the first question also the answer to the second question? If it is really true that the activity is useful to the birds in the ways and to the extent indicated, is not this proof positive of the effectiveness of the activity? Undoubtedly it is. But while the result for the first question is an answer for the second also, it is only a partial answer. The answer to the first question is the answer to the second only insofar as the California Woodpecker's nutritional activities are compared with the same activities of *other woodpeckers*. The answer to the first question gives no direct information about the efficiency of the action as considered *within itself*. From the answer to the first question we get no light on the effectiveness with which the activity accomplishes the ends *in detail* which it obviously accomplishes *in general*. The effectiveness of all the activities of living organisms has to be judged partly by the extent to which each particular act accomplishes the end for which the class of acts is performed. Driving the blood to all parts of the body is the purpose of the contractile activity of hearts, and if on any account this activity is performed imperfectly blood distributing is inefficiently done and the possessor of the imperfectly acting heart suffers. That the hearts of *A*, *B*, *C*, and *D* act efficiently is no assurance that the heart of *E* acts thus. Nor is the fact that *A*'s heart acts efficiently today assurance that it will so act tomorrow. So is it with any functional activity of any organic being.

Enough results of the detailed studies on the storing activities of these birds will be presented to bring out sharply two divergent types of fact concerning their efficiency as just defined. First, the activities show a considerable degree of pliability with reference to different conditions under which they are performed. They are to a considerable extent adaptive within their own class as well as between their class and the class of nutritional activities of other woodpeckers. But, second, side by side with this adaptiveness of the activities in certain respects there occur striking failures of adaptiveness in other respects.

Evidence of four ways in which this intrinsic adaptiveness manifests itself will be briefly discussed: (1) in sizing the holes made for individual acorns to correspond to different sized acorns; (2) in selecting those acorns which from size and shape can be most conveniently managed when nuts differing in this respect are concerned; (3) in a measure of selection of storage places on the basis of the relative ease with which the storage holes can be made; (4) in shelling the nuts, whereby the halves into which the meats readily di-

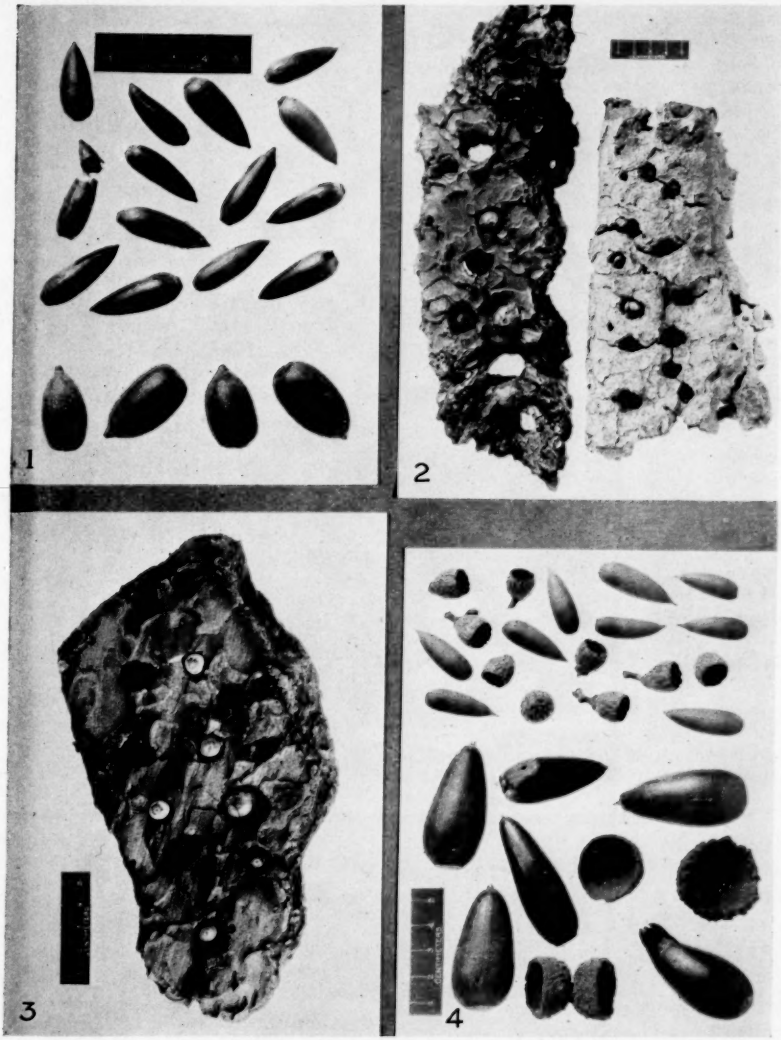

FIG. 1. ACORNS OF BLACK OAK (*a*, LOWER) AND LIVE OAK (*b*, UPPER) TO ILLUSTRATE DIFFERENCES IN SIZE AND SHAPE

FIG. 2. BARK OF (*a*, LEFT) YELLOW PINE WITH LARGE HOLES CONTAINING ACORNS OF BLACK OAK; AND OF (*b*, RIGHT) SYCAMORE WITH SMALL HOLES CONTAINING ACORNS OF LIVE OAK

FIG. 3. BARK OF YELLOW PINE WITH LARGE HOLE CONTAINING ACORN OF BLACK OAK, AND SMALL HOLES CONTAINING ACORNS OF LIVE OAK

FIG. 4. ACORNS OF VALLEY OAK (*a*, LOWER), AND LIVE OAK (*b*, UPPER) SHOWING COMPARATIVE SIZE AND SHAPE

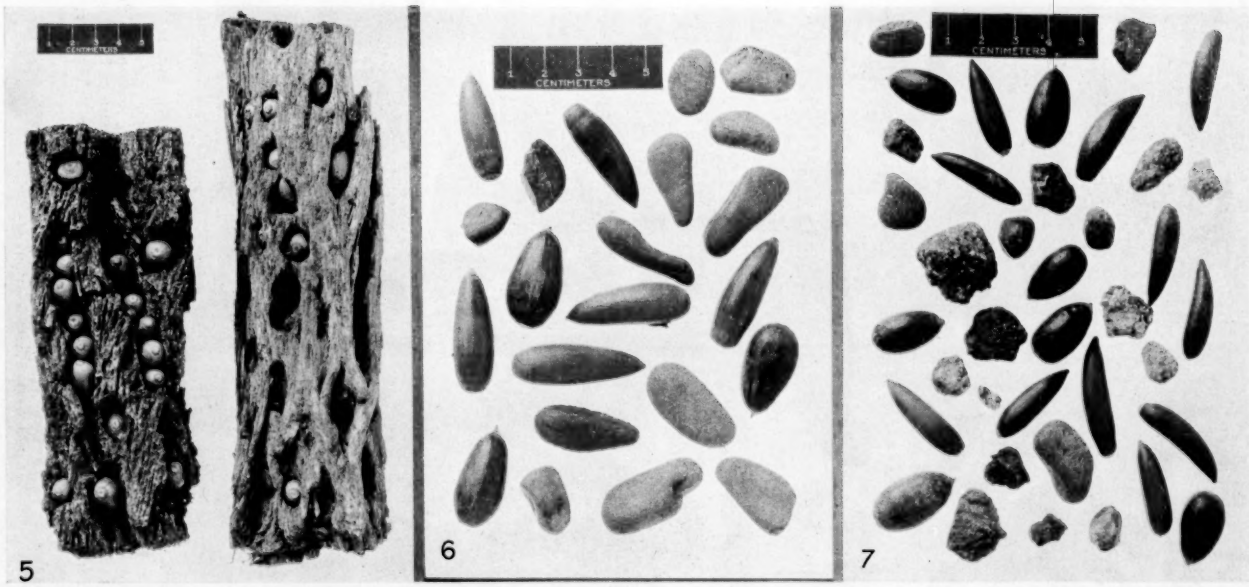

FIG. 5. BARK OF EUCALYPTUS ROBUSTA (*a*, RIGHT) SOFT, CONTAINING ACORNS STORED MOSTLY IN HOLES; AND (*b*, LEFT) E. SIDEROXYLON, HARD, CONTAINING ACORNS STORED MOSTLY IN NATURAL FURROWS

FIG. 6. ACORNS AND PEBBLES COLLECTED FROM THE GROUND WHERE THE NUTS HAD FALLEN, SHOWING CONSIDERABLE RESEMBLANCE BETWEEN TWO KINDS OF OBJECTS

FIG. 7. ACORNS AND PEBBLES COLLECTED FROM THE SAME TELEGRAPH POLE WHERE THEY WERE STORED BY THE WOODPECKERS, SHOWING LITTLE RESEMBLANCE

vide can be more effectively managed than the whole nuts can be. These we examine seriatim.

ADAPTATION OF SIZE OF HOLE TO SIZE OF ACORN

(1) That to a certain extent the size of the holes is made to correspond to the size of the acorns placed in them I have previously shown (Ritter, 1922, p. 116 f). For brevity's sake nothing more will be said about the evidence there produced. The presentation of new and more conclusive evidence can be facilitated by the photographs reproduced in figures 1, 2, and 3. Figure 1 is of acorns of the Black oak, 1 *a*, and Live oak, 1 *b*, these having all been taken by myself from the same storage tree. The average length and thickness, respectively, of the four Black oak nuts here shown is 30 mm. and 15.5 mm. These figures would certainly be nearly the same for great numbers of nuts of these oaks growing in localities and associations favorable for the birds. The same measures for the fourteen Live Oak nuts shown are 27.3 mm. and 9 + mm. There is much more variation, according to my observations, in the nuts of the Live oak, than in those of the Black oak. Nevertheless, these figures would be fairly representative for trees in localities and associations with which we are concerned.

Turning to the sizes of the storage holes and taking as samples those in the two pieces of bark shown in figure 2, we have the following figures: For the eight holes of 2 *a* the average is 14.5 mm. in diameter and for the thirteen holes of 2 *b*, 9.1 mm. Bringing nuts and holes together in the combinations that the birds make, we have this: The 14.5 mm. holes shown in Figure 2 *a* are for storing Black oak nuts of 15.5 mm. thickness and the 9.1 mm. holes of 2 *b* are for storing Live oak nuts of 9 + mm. thickness. While these statements are justified by the facts actually presented certain additional facts need to be noted, to dispose for one thing, of the difficulty that the holes containing the larger nuts seem to be actually somewhat smaller than the nuts. This may be due partly to the insufficient number of nuts and holes measured and to inaccurate measurements. But it is due more, probably, to the fact that in neither of these sets of measurements were the nuts and the holes from the same locality. The Black oak (large) nuts shown and measured are from Cuyamaca while the large holes shown and measured are from Keen camp on San Jacinto. The Live oak (small) nuts are also from Cuyamaca, while the small holes are from "Shady Nook" on a branch of the San Luis Rey river.

The justification for this criss-crossing of data as a convenience in presentation will be seen presently. It was indulged in from confidence that it would not seriously affect the results. My collections contain a large number of Black oak nuts that were actually taken from holes in the same bark shown in figure 2 *a;* and these differ too slightly from the four Cuyamaca specimens to have any recognizable influence on the quantitative results as presented. Similar remarks would hold for the Live oak nuts and the holes in which they occur.

It should be remarked that the samples collectable in this way are far less impressive than are the facts as seen in the field. This applies especially to the holes shown in figure 2. It will be understood that collecting specimens of bark from standing trees, live ones particularly, is not a simple matter. The dead, dry trunk from which figure 2 *a* was taken contained many—several scores at least—of holes similar to those shown.

A live sycamore near the one from which figure 2 *b* was taken contained easily several hundred holes, most of them having nuts, all of the Live oak. The uniformly small holes, each with its tight-fitting nut, was striking indeed.

We turn now to the specimen shown in figure 3. A glance is enough to reveal two distinct sizes of nuts and holes. The single large nut toward the right is a Black oak. The five smaller ones are Live oak. Everything is as it was while the piece of bark was on the tree—a yellow pine—the individual being the one from which the nuts measured, and shown in figure 1 *a* and *b*, were taken. As already noted, this specimen is from the middle slope of Cuyamaca, where Black and Live oaks and Yellow pines are freely mingled.

The evidence, then, is ample to prove that *within limits* the storage pits made by the California woodpecker correspond in size to different sized acorns stored in them. Before leaving the point attention should be called to the emphasis placed on "within limits." Although adaptiveness here is beyond question, it is far from perfect. But full discussion of this aspect of the subject must be omitted.

SELECTION OF EASILY HANDLED ACORNS

We now pass to the second way in which the activity shows adaptiveness: In a situation where acorns of different sizes

are presented, those are to a certain extent selected which are of a size most easily handled by the birds. The acorns of two Quercine species utilized by the woodpecker at their maximum size are very near to, even if not a little beyond, the grasping capacity of the bird's beak. The beak is the only means the creatures have for "handling" (really for "beaking") the nuts; nor have the nuts anything in the way of a "handle" (beakle?) that can be grasped. The oaks referred to are the Valley oak, (*Q. lobata*) and Maul oak (*Q. chrysolepis*). Nuts of the first having a thickness of 26 mm. and a length of 48 mm. are not uncommon. And this species is one of the most commonly used of all the oaks. The normal opening at the tips of the mandibles as measured on one individual was 17.5 mm. Stretched to near the limit the measure became 25.5 mm. Thus it is seen that the larger nuts of the Valley oak can hardly be grasped whole. And the smooth, slippery surface of the nuts must increase the difficulty of holding the larger specimens.

I have no measurements of the acorns of the Maul oak; but certain it is that at their maximum they are at least as large as the largest of the Valley oak nuts. But this oak enters much less into the careers of the birds than does the Valley oak. I recall but two cases in which these nuts had been fed upon and only one in which they had been stored.

Since the selective action with which we are now concerned involves the Valley and the Live oaks almost exclusively, only these will enter into the rest of this discussion. Figure 4 *a* and 4 *b*, respectively, show clearly the size differences of these acorns. The evidence of selection as between the nuts of these oaks is that almost without exception where the two species mingle, I find the Valley oak used much more as granaries, while the nuts of the Live oak enter much more into the stored-up material. This is the rule to such an extent that it seems unnecessary to go into details. But the Diablo, the Ojai, and the Eden Dale Farm settlements may be mentioned as particularly good illustrations. Other possible explanations of the selection than that of size suggest themselves: May not the greater abundance of the Live Oak (smaller) nuts be the determining factor? It is impossible on the basis of present information to rule out this factor. The point involves, for one thing, the question of the relative fruitfulness of the two oaks. But according to Jepson (1910, p. 209) the Valley oak "bears more abundant crops of acorns than any other West American oak." My observations confirm this. Hardly, then, can greater abundance of the smaller nuts due to greater fruitfulness of the trees be a factor. But the possibility of more Live oak nuts from the presence of more Live than of Valley oak trees would have to be considered.

This, however, would not account for the fact that one often finds a Valley oak tree bearing a good crop of acorns stored with many Live oak acorns which must have been brought from distant trees.

Again it may be surmised that the Live oak nuts answer the food needs of the birds better than do the Valley oak nuts. For instance, is it not likely, one may ask, that the taste of the Live oak nuts is more to the birds' liking than that of the Valley oak nuts? This query is particularly relevant since the idea that the birds show a preference for the sweeter kinds of acorns occurs here and there in the literature. We surely have no evidence that one kind of acorns is better food for the birds than any other kind. As to the relative "sweetness" we have no criterion to go by but our own taste and for us the Valley oak nuts are distinctly sweeter. The evidence is, then, almost conclusive that the selectivity as to the kinds of nuts is on the basis of size.

SELECTION OF SOFT BARKED TREES FOR STORAGE

The form of adaptivity next to be noticed concerns the objects utilized as storage places. The relative hardness of the objects is the chief thing here. Nowhere does the point come out more definitely than in connection with those arboreal associations where soft-barked trees like the Yellow pine are mingled with hard-barked trees like the Black oak. In such cases I have yet to find an instance of departure from the rule that the pines are the granaries to the practically complete exclusion of the oaks. This is the more noteworthy because the oaks are abundantly so utilized in localities where there are no pines, as for instance where the Valley oaks or the Live oaks occur either alone or associated with each other. But even in these cases the rule as to hardness holds. Attention was called under the preceding heading to the fact that in Valley oak—Live oak associations, the Valley oaks are the chief storage trees. This is correlated with the greater availability in several

ways of the Valley oaks for storing. For one thing the extensive ridge-and-valley structure of the bark of old individuals of this oak furnishes not only many nooks and crannies for storing with little or no bark picking required but also especially favorable conditions for regular hole drilling. The relatively even surfaced bark of the Live oak, to say nothing of its hardness, seems quite forbidding to hole making.

A striking example of this form of adaptiveness is presented by the resort of the birds to Eucalyptus trees for storing. Several instances of this are known, but far the most notable one known to me is near Santa Barbara and still nearer Montecito. Figure 5 *a* and *b* illustrates what has happened here. A rather extensive grove consisting chiefly of *E. robusta* and *E. sideroxylon* has been planted in a narrow valley in which Live oaks abound. The bark of *E. robusta*, 5 *a*, is thick, much ridged, and exceedingly soft and friable, while that of E. *sideroxylon*, 5 *b*, though likewise thick, is much harder. Both species are much used for storing. But, as a glance at the figures reveals, while most of the nuts stored in bark of *robusta* are in holes made by the birds, most of those stored in the bark of *sideroxylon* are in natural channels. Attentive comparison of the work done on these two kinds of bark discovers that whereas most of the preparation of the harder bark for storing has consisted in a little rimming out, so to speak, of the natural, narrow grooves to receive the nuts, most of that done on the softer bark has consisted in actual hole drilling.

When it is remembered that Eucalypts are very new comers, relatively, into the birds' environment, and that until their arrival no such sharp alternative as to soft and hard media for storage holes were presented to them, the case stands out strikingly as an example of adaptiveness in activity. For having my attention called to this interesting case and for the opportunity to study it, I am indebted to Mr. Ralph Hoffmann, author of a recent book (1927) on Pacific Coast birds.

Before leaving this topic it is desirable to refer more specifically to the use made by the birds of cracks of various kinds and in various situations for storage purposes. For instance the shrinkage cracks which develop extensively in dead and decorticated parts of trees, and in wire-line poles are much utilized. That this is connected in several ways with the general problem of the adaptiveness of the storing activity there is no doubt.

SHELLING OF ACORNS

The fourth and last form to be discussed of intrinsic adaptiveness exhibited in the storing activity concerns the shelling of the nuts. My attention was called to this by Mr. C. W. Michael, who seems to have been the first to observe it. Since this phase of the activity came to my notice I have been on the lookout for it. In two instances during my field trips in company with Mr. Burt we have found shelled and halved meats of acorns stored in deep cracks along with whole nuts. Almost certainly this was in both cases the work of the California woodpecker. But since Mr. Michael's observations furnish much the best evidence we have on the point, I confine myself to this source, giving most of it in the observer's own words as communicated to me by letters from the Yosemite Valley under dates of December 2 and 13, 1928:

"On the morning of December 2, 1928, I saw an individual California woodpecker, the same individual, and he was never out of my sight, gather and crack two acorns. This same individual was seen to store four half acorns. However, the dead limb which he used as a vice when hulling acorns was some fifteen feet above the ground and from where I stood I could not be positive that the half acorns that the woodpecker carried away and stored were already hulled acorns in the vice. . . . . In this particular case it was not the least difficult to follow the movements of the woodpecker under observation for he did not move far. He picked up acorns on the lawn, flew to the limb used as a vice, and then to the eaves [of a dwelling house] where he was storing. Never was he more than 100 feet from me." A few additional details are given in another letter. "The operation of gathering, shelling and storing the two halves was completed in slightly less than five minutes."

The entire process was followed in only one bird. But since at least ten others were at work at the same time, the storing act proper being seen in some of these, Mr. Michael felt sure that other individuals were doing essentially the same things. While, as stated, the performances most completely followed stored the nuts in the eaves of the building, other nuts were put into cracks between the shingles of the main roof. Although the observed facts are not sufficient to justify the assertion that the shelling and halving had as its direct, immediate end the storing of pieces in niches too small for the whole nuts, there seems no doubt that the pieces could at least be more easily handled than could the wholes. The tree concerned is the Black oak, the nuts of which, it will be recalled, are considerably larger than those of the Live oak.

Another point mentioned by Mr. Michael is that the nuts on the ground from which the birds were making their collections, were found to be splitting open in many cases—owing undoubtedly to the wet-

ting they and the ground had received from the winter rains and snows. This fact, illustrative of a rule for fallen nuts this late in the season, must greatly facilitate the task of shelling. Along with these considerations it should be noticed that these birds seem never to swallow the acorns meat, shell and all, as is the way with some creatures, e.g., the Band-tailed pigeon and the Mule Deer. This means that opening the nuts in one way or another is part of the task of preparing the food. Undoubtedly this must come into the reckoning along with that of storing the shelled pieces. But even so a large measure of adaptiveness is unmistakable in the operation.

To sum up, the food storing activities of the California woodpecker manifest intrinsic adaptiveness in four particulars: in fitting storage holes for acorns of different size; in selecting nuts of convenient size for handling; in selecting storage objects on the basis of greater and lesser resistance to hole drilling for the nuts; and finally, in shelling nuts, thereby gaining advantages in managing parts of nuts instead of whole ones. This is the answer to our second primary question, that of the effectivensss of the activity when this is viewed from the inside. From the general nutritial standpoint it shows considerable effectiveness when its own particular acts are compared among themselves.

MALADAPTIVITY IN STORING

But fidelity to truth and fullness compels us to recognize that side-by-side with the observed facts which lead to the conclusion as stated there are other facts of quite different purport. Some of the most conspicuous of these will now be examined. I have discussed certain aspects of this matter elsewhere (Ritter, 1922, p. 109f, and 1928, p. 128f), using the term maladaptivity for the types of activity described. I will restrict the presentation here to three of the most positive types and give factual information gathered since the publication of the earlier discussions. These will be: (1) the storing of objects that are entirely useless as food: (2) the storing of valuable food objects where they can not be recovered by any means available to the birds; (3) the pecking of holes that are either unusable for storing or, though usable, are not used.

STORING OF OBJECTS USELESS FOR FOOD

(1) The following is a list of stored objects which up to now have been observed: acorns, almonds, hazel nuts, dates, Indian Corn, English walnuts, pecans, native California walnuts, seed capsules of the Eucalyptus, stones. The list is arranged with general reference to the usability of the objects as food. Acorns, of course, head the list and head it so pronouncedly as to leave no room for question that it is with these objects that the activity is primarily concerned. Almonds, occupying second place in the list, probably hold second place, now, among nuts as food for those of the woodpeckers that inhabit almond raising districts. But this, of course, could be true only for very recent times. There is considerable evidence that in some localities and perhaps in earlier years, hazel nuts were used quite extensively. The place of stones is necessarily at the other end of the list. But utterly useless as these are either as food or in any other imaginable way, the storing of them we now know to be rather common. For instance from my questionnaire and from various other sources I now have a list of at least ten instances where such storage has taken place. The phenomenon is then sufficiently characteristic of the storing activity to make it deserve careful study.

How does such an absurd perversion of a useful activity come about? The hypothetical answer which I gave several years ago was this: Assuming that acorns for storing are sometimes picked up from the ground, and that this takes place occasionally where the nuts have fallen in pebbly places (as is not infrequent) it is conceivable that the resemblance of some of the pebbles to acorns is so close as to lead the birds to mistake the one kind of objects for the other. To test this hypothesis has been one aim of my recent studies. During the last year the aim has been measurably attained. That the birds actually do collect nuts after they have fallen is testified to by so many observers that there can be no doubt about it, although gathering from the trees is the only mode I have personally observed. While on the Red Bluff trip in October last I found striking instances of acorns resembling more or less closely pebbles on the ground under the trees from which the nuts had fallen.

Figure 6 shows a sample of the collection made. While the reader will have no difficulty in distinguishing acorns from pebbles, neither will he fail to see considerable similarity between them.

Fortunately, not many miles from where this collection was taken an old wire line pole richly stored with both acorns and pebbles was found. This gave a chance to see how much resemblance there was between the two kinds of objects. Figure 7 shows the two mingled as in the previous case. No one can fail, I think, to see that acorns and pebbles of figure 7 resemble each other less than do those of figure 6. In fact the pebbles stored by the birds are about as unlike the acorns stored with them as could be

other mineral matter. Perhaps the change from animal to rather hard vegetable food has been accompanied by the taking of a certain amount of gravel to aid in triturating the food—something after the fashion of the utilization of gravel by some graniverous birds. Should this surmise prove correct still another adaptation in connection with the acorn habit would have to go to the credit of this woodpecker. More field observations, supplemented if possible by experiments, are necessary for testing these guesses.

The whole problem of utterly futile activity by animals is here touched upon but does not enter into the aim of this paper. That here is an instance in

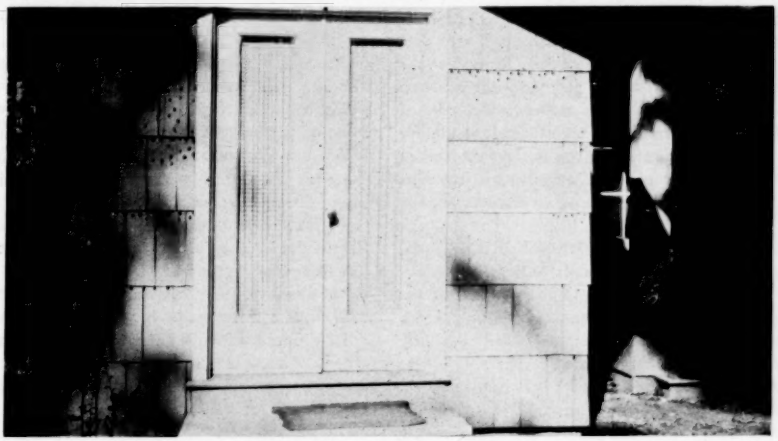

FIG. 8. PORTION OF END OF A COTTAGE AT MT. DIABLO COUNTRY CLUB SHOWING HOLES MADE BY THE WOODPECKERS, MOSTLY COMPLETE BUT SOME INCOMPLETE

gathered. This comes out more sharply on the samples themselves than in the photographs, since diversities of color as well as of shape and size figure in the comparison. The evidence, then, tends strongly to disprove my hypothesis that pebble storing is due to mistaken resemblance, if resemblance is understood in any detailed, critical sense.

Another explanatory hypothesis of the phenomenon is given by Henshaw (1921). He suggests that pebble storing is done in seasons when, or localities where, the acorn crop is more or less of a failure. Under such conditions the poor birds store pebbles as a substitute for nuts!

Still another possible significance of the phenomenon is suggested by the discovery that the stomachs of the birds may contain liberal quantities of gravel and

which the real end served by an activity is entirely missed is so obvious as to need no dwelling upon. My only discursive remark on the subject is that the impression made on a free minded observer is that the birds have a general activity-set toward picking up objects and storing them away and that this is stimulated into action by almost any objects which are at all amenable to such action.

It is doubtful whether the seed capsules of the Eucalyptus and the almost stony hard nuts of the native walnut (*Juglans californica*) are more available to the birds as food than are pebbles. I should expect that objects of any kind whatever of manageable size, copiously strewn among fallen acorns from which collections were being made by the birds, would get a place in their garnered material. The

phenomenon is, I take it, the same in general character as that of the great variety of absurd objects on which brooding birds will sit (see Kirkman, 1927, p. 863).

STORING OF FOOD WHERE IT CANNOT BE RECOVERED

We next consider the storing of good food objects where they can not be recovered. An instance in point is indicated in figure 8. The cottage here shown is on the grounds of the Mt. Diablo Country Club. The numerous holes appearing in the shingles, or shakes, are the work of the woodpeckers. This building is sheeted inside as well as outside. Consequently many of the perforations open freely into the space usual to this form of construction. What may happen in connection with the acorn storing business here tells its own story. The case is presented as a real example of what is not rare in California and is familiarly regarded as a joke played by the birds on themselves. Mr. Leach tells me that the wall of this cottage has been opened several times to remove the accumulated acorns; and that the quantity taken out may be well toward the bushel mark, the nuts being in various stages of decay or consumption by insects and mice.

An instance reported by Mr. John Ultringham, living in the country near Lodi, California, is even more to the point. The continued activity of the woodpeckers around a particular telephone pole attracted Mr. Ultringham's attention. Looking into the matter this is what he found. The pole bore a conduit pipe from which the wires had been removed. The birds were dropping articles into its upper end. Further examination found a pile consisting of acorns, almonds and walnuts under the lower end which opened a foot and a half or more from the ground. Thinking to test the "industry" of the birds, Mr. Ultringham put a fruit picker's bucket under the pipe. This was filled several times in the period during which he watched and emptied it. The nuts were not put where the birds could not get them in this instance. But what was gained by dropping their food through the pipe, assuming they expected to eat it at some future time, is hard to see. Although this story does not come from a woodpeckerologist, there is no reason to question it. So in keeping is it with much that the birds certainly do that they might well have done the thing reported, even if they didn't.

To give all the details of this sort contained in my notes would consume time and printer's material, beyond any informative value it would have. On one question which may be raised something should be said. Is this form of nutritial maladaptation restricted to situations which have been imposed, so to speak, upon the birds by the coming of man into their environment? The evidence is conclusive that it is not. From the abundance of such evidence I will present only two instances. One is furnished by Peck (1921). This I have referred to in previous publications, but it is sufficiently striking to warrant mentioning again. Although Peck's observations were on a different subspecies (*Balanosphyra f. albeolus*) and were made in British Honduras, the point under consideration is not essentially altered thereby, I am confident. The kernel of the case, stated in the observer's own words is: "I have seen a hollow pine tree with a cavity six or eight inches in diameter filled for a distance of nearly twenty feet with acorns dropped into a good-sized hole at that distance above the ground. Acorn-filled trees of this sort I found not uncommon. Sometimes an opening at the bottom showed the earlier acorns deposited completely decayed and crumbling to dust."

An equally natural but less striking instance of a like kind came to my notice at Keen Camp on San Jacinto mountain during my work there in June, 1928. Some of the bark of a dry pine stub (the one from which the piece shown in figure 2 was taken) had sloughed off entirely while other portions were so loose as to be separated from the wood by a considerable space. One of these pieces which was still adherent at its lower end some two or three feet down, had been abundantly punctured by the birds. Most of the holes in this piece went entirely through the bark. As a consequence the acorns put into these holes dropped down in the space between bark and wood. The accumulation of lost nuts, perhaps a quart, I happened to find from pulling off the loose slab of bark for a specimen.

ABORTIVE HOLES

The third and last form of uselessness of the activity concerns the holemaking itself. Here again to save time and space I will do no more than add to the evidence previously given in my *Condor* articles that great numbers of holes are made into which no acorns or anything else are ever put. The additional point in this aspect of the matter I will now emphasize is that innumerable of these uselessly made holes are useless from the simple fact that they are not made large and deep enough to receive the nuts. The point is illustrated in the photographs of the bepunctured cottage of the Diablo Country Club (fig 8). It will be readily seen that the spots on the shingles vary greatly in size, some of them being only a little above visibility. A bit of evidence from this cottage is presented in tabular form (see table 2, page 482).

On this exhibit slightly less than 55 per cent of the holes are large enough to receive nuts. But this is hardly fair to the birds. As to size of holes they

certainly have not here wasted 45 per cent of their work. For instance in this case had I counted all the holes in all the shingles many would have shown presumably fully abandoned abortive holes is not here large. The whole instance is however truthfully illustrative of an extensively performed kind of

MAP
OF
CALIFORNIA
Showing the mountain ranges and river systems of greatest importance in relation to the geographical distribution of the native trees, with the county boundaries and chief towns.
MILES

FIG. 9. MAP OF CALIFORNIA, AFTER JEPSON (1910)

what the 8th shows, namely all the holes full sized. Furthermore, as the table indicates many of the abortive holes were fresh. This means that later the birds may complete them. The percentage of old and hence futile activity. A good example is furnished by a wireline pole in the same neighborhood. This pole is thickly marked from bottom to top by the hole-making industry. There are certainly several hun-

dred of these marks. And certainly, too, less than half of them are deep enough or broad enough to admit even the smallest acorns. And all the work is old. There is nothing to suggest the possibility that the job is to be completed after a while. Yet the birds are all around here, undoubtedly alighting frequently on this very pole.

A customary view about the abortive holes is that they are unfinished in the sense that a ditch or a tree-planter's or a well-digger's holes in the ground must of necessity be unfinished part of the time. Or in particular situations such as this cottage presents, where people, dogs, cats, etc., are apt to come along, the supposition is that the birds were driven or scared away from their tasks. Another explanation favored by some naturalists is that such work is exploratory or trial. By this view it is placed in the category of the gold miner's prospect-hole or the oil man's prospect-well.

TABLE 2

SHINGLES	TOTAL NUMBER OF HOLES	FULL SIZED HOLES	ABORTIVE HOLES
1st	12	3	all old
2d	8	3	all fresh
3d	7	4	all fresh
4th	16	10	all fresh
5th	9	4	all fresh
6th	19	11	all fresh
7th	9	4	all old
8th	10	10	

But after allowance is made for explanations of this sort, it is, I believe, demonstrable that a great amount of activity performed not only by these woodpeckers, but by many other animals, is utterly futile judged on the basis of the obvious usefulness of the activity *as a type*.

The display of abortive holes in the Diablo cottage is no greater than can be seen in innumerable other cases where none of the above mentioned common explanations can be positively shown or even reasonably supposed to be operative.

The most convincing evidence for the contention that a considerable part of the hole-making activity of the California woodpecker fails to attain the end it typically does attain and so is adjudged futile, can be got by watching the birds at work.

I give a single instance from my Yosemite Valley trip of November-December, 1928. But preliminary to the narration reference should be made to Mr. Michael's belief that the woodpeckers of the Valley have largely abandoned trees as acorn storing places and have taken to wooden buildings, largely for the purpose, he believes, of utilizing cracks into which by a little enlarging the nuts can be thrust. I have considerable personal observational evidence confirmatory of this view. Certain it was that no tree storing was observed during my late visit, yet the birds were abundant and very active. And no small part of their activity was pecking—mostly on dead, dry, barkless branches of the Black oaks.

As seemingly typical of this work take the following from my field notes: "Bird working on side of a limb in full view. Five fresh pits in a row, one apparently large enough for a nut. None of the others deep enough. Bird worked alternately in two or three of these, then went away." There was nothing recognizable in the situation to explain the cessation of pecking. The bird was merely acting in a general way like a dozen or more others in the immediate vicinity. Certainly one can imagine that this individual, perhaps like others which had previously worked at the same pits (I was almost sure the bird watched did not begin any of them, at this "shift" any way) decided there was something wrong about the place. Or he can imagine that the individual went away to get something to eat or to do something or other with some other individual with the intention of returning after a while to finish the job. And several other more or less plausible explanations can be imagined. But since the case itself furnished no observational evidence for any of them, it seems useless to entertain them. Conclusive evidence that innumerable holes are started and never finished is supplied by the fact that weathering and other unmistakable signs of age are upon them.

SUMMARY

A final summing up of the results of this study may be given thus: California woodpeckers promote their own welfare as this depends on food by the use they make of their heads, in at least two ways: (1) they somewhat extend, as compared with neighboring species of woodpeckers, the range of their most vitally influential external conditions of life; (2) they somewhat reduce, as compared with neighboring species, their rate of mortality as shown by their increased ratio of adult population to their reproductive capacity.

This greater effectiveness of their nutritial activities as compared with those of neighboring species may be designated as

extrinsic evidence of adaptiveness of the activities.

Attentive study of the activities discovers them to vary considerably with the somewhat varied external conditions under which the birds live. Four kinds of external conditions to which the activities conform more or less are presented in the study. This sort of thing may be designated as *intrinsic evidence* of adaptiveness of the activities.

But the studies which secure this intrinsic evidence of the activities' adaptiveness can hardly fail to discover sharp limitations to this adaptiveness. Three kinds of such limitations are presented. They are designated as *maladaptations* of the activities.

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THE CYTOLOGY OF GLANDULAR SECRETION *(Continued)*

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THE RÔLE OF THE CYTOPLASM IN SECRETION

For the cytologist, at least, the problem of the origin of secretory products is thus definitely located in the cytoplasmic area of the cell.

Bowen, 1924.

THE attempt to find a nuclear basis for secretion having eventuated rather dubiously, many workers have concentrated their attention on the cytoplasm. In some cases nuclear activity has been definitely eliminated, in others nuclear cooperation has been held possible or necessary. The earlier accounts of changes in cytoplasmic appearance accompanying secretion frequently speak only of a "mucous degeneration," or in other ways derive the secretion droplets from the general cytosome (Paneth ('88), Yamanouchi ('22), and many other references given on page 305). Such meaningless statements have long since been abandoned with the unfortunate exception of some holocrine glands, as already noted on page 304. It is now clear that a satisfactory explanation of the origin of a secretory droplet must be reduced to more concrete terms. To accomplish this, appeal has been made to practically all of the formed components of the cytosome, with results which will be reviewed in the following pages.

The granule doctrine

Das Grundgesetz des Secretionsprocesses also ist überall dasselbe: überall haben wir es zunächst mit den primären Granulis zu thun, ... ; die aus diesen primären Granulis heranwachsenden und heranreifenden Secretkörner liefern die specifischen Bestandtheile des Secretes.

Altmann, 1894.

Danach würde die erste Entstehung der Granula einfach darauf hinauslaufen, dass kleinste, metamikroskopische, lebende Teilchen einen gewissen Grad der Selbständigkeit erlangen und durch Assimilation, Wachstum und entsprechende Metathese ihrer Substanz sich in die histologischen Granula umwandeln.

M. Heidenhain, 1907.

Of the cytoplasmic structures we may conveniently take account first of the ultimate particles into which living matter is presumably divided, taking our departure from the granule theory of protoplasmic structure associated with the name of Altmann ('94). According to the granule doctrine, living matter consists of a congeries of discrete particles each of which is 'alive,' and can by hypothesis grow, divide, and differentiate itself into this or that cellular product. According to Altmann ('94), a secretory droplet arises by the mere growth of one such granule or bioblast, which eventually achieves the transformation chemically necessary for a particular secretion (compare also with the section on chondriosomes, page 488). This view has been developed by M. Heidenhain ('07), who derives secretory granules directly from the ultimate, submicroscopic, living particles or "protomeres," out of which he considers protoplasm to be constructed. His point of view is admirably stated in the sentence at the head of this section. Other workers (Müller ('96, '98) Noll

('01), Jurisch ('09); compare also Saint-Remy ('92)) have sought a similar escape from the difficulties of tracing the exact relation of a secretion to any previously visible component. Secretory granules have a disconcerting way of emerging into visibility apparently from nowhere—in which respect they but emphasize the universal sense of defeat which everyone must feel who attempts to account for the appearance in the cytoplasm of a formed component not previously visible. The obvious escape from such a dilemma is the assumption that a secretory droplet has emerged from a distinct formation which already existed in submicroscopic form. Thus is the whole situation deftly removed from the domain of cytological analysis, and we are left at the very threshold of the essential problem with a sense of utter futility.

That such an explanation should prove satisfactory to cytological workers is clearly not to be expected, especially when we take into account the obvious difficulties involved in the necessarily theoretical assumptions as to the ultimate structure of living matter. Most workers have, therefore, sought for a more tangible solution among the formed constituents of the cytoplasm. The results of this search must now be considered.

Protoplasmic fibrillae—The ergastoplasm

> On a admis qu'il [l'ergastoplasme] y participait directement ou indirectement. On l'a considéré comme un prézymogène, c'est-à-dire comme un premier stade chimique des grains de sécrétion définitifs. Mais aussi, n'ayant pu observer la transformation directe de l'ergastoplasme en matériaux de sécrétion, on lui a attribué une influence indirecte, et directrice dans l'élaboration de ces matériaux.
>
> Prenant, 1910.

When gland-cells—the vertebrate pancreas furnishes particularly good examples—are fixed in fluids characterized by the presence of mercuric chloride but containing no osmic acid, and are then properly stained, their cytoplasm is frequently found to contain fibrillar structures. These are primarily a characteristic of the basal end of the cell and their distribution is frequently limited to that zone; whence the term "Fussplasma" used by Jacobs ('28) after Frenzel; also called 'Basoplasma' by Roskin ('25), and basal protoplasm ('protoplasme basal') by Morelle ('27a), and many others. Such a fibrillar appearance seems to have been first clearly described in gland-cells by Eberth and Müller ('92), but the prior observations of Macallum ('91) should also be noted, and some workers credit the first description to Pflüger or R. Heidenhain at much earlier dates (e.g., Saguchi, '20a). These fibrillae were subsequently described in more detail by Solger ('94, '96, '98), who applied the name "basal filaments," and as the "ergastoplasm" of Garnier ('97, '00a, b) and Prenant (protoplasma supérieur) ('98–'99), their importance was much emphasized. In the years which marked the turn of the century, the resulting 'ergastoplasm theory' received a great deal of attention.

The exact morphology of the ergastoplasm has never been very clearly defined, and in the hands of various workers it has assumed several quite different forms. Most frequently, as the name given by Solger ('96) suggests, the ergastoplasm presents itself in the form of filaments (fig. 7*A*) (cf. Solger ('94, '96), Mouret ('95), Garnier ('97, '00a, '00b), Hammar ('97), Prenant ('98–'99), Mathews ('99), Theohari ('99), Saguchi ('20a), Lutz ('21), Krüger ('23), Roskin ('25), Jacobs ('28)) which were frequently supposed to be in some way related to the fibrillar cytoplasmic structure of Flemming's familiar theory (Solger ('96), Hammar ('97), Garnier ('00b)); while Saguchi ('20a) called them protofibrillae; and

Krüger ('23) thought the filamentous appearance was determined by the inward diffusing stream of fluid from the vascular channels. Others, however, especially among more recent workers, have considered the ergastoplasm merely as an amorphous, diffuse material located in the basal region of gland-cells (fig. 7*B*) and easily transformed into a fibrillar appearance by improper fixation (Bensley ('98, '11), Regaud and Mawas ('09a), Dolley ('25), Benoit ('26), Morelle ('27a)). Perhaps the ergastoplasm should include (e.g., Laguesse ('11, '24), Lutz ('21), and especially Morelle ('27a)) the various nebenkern-formations described by Nussbaum ('81) and many later writers and already discussed on page 320. The point which seems to have been relied upon to bring all these divergent structures under the heading 'ergastoplasm', is their common affinity for basic stains. Many earlier workers traced this staining reaction to a supposed contribution of nuclear chromatin drawn off from the nucleus by the ergastoplasmic threads (Mathews '99, Garnier '00a). Other workers describe the nuclear contribution in various terms (cf. Conte and Vaney ('02), Launoy ('03), Regaud and Mawas ('09b), Brinkmann ('12), Millot ('26)), while Dolley ('25) considers the ergastoplasm as equivalent to chromidia (see page 321), a relationship categorically denied by Lutz ('21). On the other hand, any relation to the nucleus has been absolutely denied in other instances (Limon '02, Lutz '21, Roskin '25, Jacobs '28). On the whole, the most tangible feature of the ergastoplasm seems to be its alterations in amount (and staining capacity) at different parts of the secretory cycle. Thus, in cells actively synthesizing secretory droplets, the ergastoplasm is fully developed while in cells

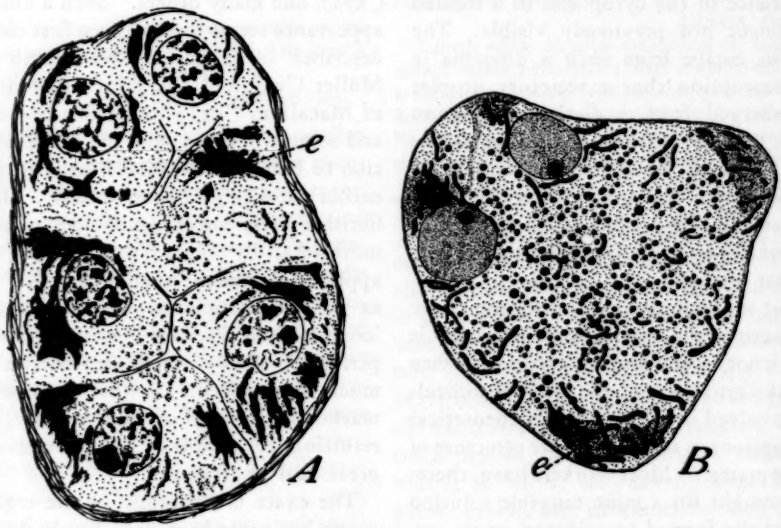

FIG. 7. THE ERGASTOPLASM IN GLAND-CELLS

A, fibrillar type in the submaxillary gland of man, from Garnier, 1900; *B*, amorphous type (rod-like bodies are chondriosomes) in the submaxillary gland of man, from Regaud and Mawas, 1909. *e*, ergastoplasm.

loaded with secretion it is greatly reduced or entirely absent (cf. Garnier ('00a, b), Prenant ('98–'99), Jacobs ('28), and many others).

Exactly how the ergastoplasm is connected with secretory activity has never received any very definite explanation, even from those who were its most ardent advocates. Almost no one has described an actual transformation of the ergastoplasmic fibrillae directly into secretory granules, a procedure definitely excluded by Eberth and Müller ('92), Garnier ('00a), and Regaud and Mawas ('09a) (but see Mouret ('95), and Theohari ('99)), although such a description of the fate of the nebenkern has been occasionally given. Usually the development of the ergastoplasm has been viewed as in some sense precedent to the synthesis of the secretory substance proper (Solger ('96), Garnier ('97, '00a), Laguesse ('99), Mathews ('99), Limon ('02), Bensley ('11), Brinkmann ('12), Lutz ('21), Dolley ('25), Benoit ('26), Jacobs ('28)).

The reduction of the ergastoplasm concept to a concrete statement is, therefore, a practical impossibility. The facts seem only to warrant the idea of an ill-defined substance of basophilic nature located toward the base of a gland-cell (the 'cell-portal,' Benoit, '26) and connected in some way with the production of secretory products. The very indefiniteness of the ergastoplasm-concept and the fact that it is so well demonstrated after technical methods certainly known to be destructive of cytoplasmic structure, early led to doubts of its status as a legitimate cell-element. The development of the chondriosome theory dealt the idea of ergastoplasm a very serious blow, and it was soon pointed out that in all likelihood the ergastoplasm was merely poorly fixed chondriosomes. In the end, Prenant ('10), himself one of the foremost proponents of the ergastoplasm theory, frankly admitted that this was probably the truth. Others have viewed the matter in the same light (e.g., Bouin ('05), Champy ('11), and Mislawsky ('13) (in part)), and Laguesse ('24) has developed a very complicated sequence involving a cycle of nucleolus-ergastoplasm- chondriosome- secretory granule.

Nevertheless, many recent workers have not accepted Prenant's surrender of the ergastoplasm, and the presence of a special basophilic or chromophilic substance is still believed by some to be coexistent with the quite different chondriosomes (Regaud and Mawas ('09a, b), Bensley ('11), Saguchi ('20a), Lutz ('21), Dolley ('25), Benoit ('26), Millot ('26), Jacobs ('28), Ma ('28)). Some of these workers (Saguchi, '20; Jacobs, '28) still interpret the ergastoplasm in fibrillar terms, but the majority opinion seems to be that it is an unformed material which is easily rendered fibrillar by fixatives which are too strongly acid. Fixatives of the type (non-acid) now accepted as essential for cytoplasmic study usually yield preparations in which the basal substance is not fibrillar. The essential facts were indeed largely grasped by Bensley as long ago as 1898, and the full rôle of the fixative has since been made known by several workers (Bensley ('11), Dolley ('25), Morelle ('27a)).

Whatever status, therefore, may be finally assigned to the ergastoplasm, it seems reasonably certain that the remarkable fibrillar structure of the classical accounts is of very doubtful reality. It appears more and more probable that two quite different things have been confused under the name of ergastoplasm. One of these is only a remnant of the poorly fixed chondriome and represents the fibrillar material as Prenant conceived it. To this extent the ergastoplasm problem comes more prop-

erly under the head of the rôle of chondriosomes in secretion (q. v., infra). The other is a specialized protoplasmic region in a gland-cell expressive of the special activity in the basal zone, where the incoming materials from the capillaries must be particularly concentrated, and where perhaps they undergo the first steps in secretory synthesis (Benoit, '26). Such activity is perhaps reflected in the distinctive staining capacity of the basal zone. To this extent the 'ergastoplasm' would represent one phase of the secretory activity of the cell as a whole, and in some such indirect rôle, if any, the ergastoplasm must now apparently find its interpretation. At all events it is at present clearly impossible to develop from the ergastoplasm any useful explanation of secretory origins. For those who might have some special interest in this problem, I might add that few subjects have been so adequately or frequently reviewed as the ergastoplasm, and the voluminous literature is discussed by several authors in much more detail than has been possible in this place; cf. Eberth and Müller ('92), Solger ('96), Garnier ('00a), Laguesse ('05–'06, '11, '24), Prenant ('98–'99, '10), Saguchi ('20a), Lutz '(21), Roskin ('25), Benoit ('26), and Morelle ('27a).

The chondriosome theory

. . . . ce rôle du chondriome s'établit d'une façon très simple: les chondriosomes se transforment directement en grains de sécrétion.

Hoven, 1912.

una continuità materiale, . . . fra i condrioconti e quelli che abitualmente son ritenuti i prodotti dell'attività metabolica della cellula, non esiste.

Levi, 1912.

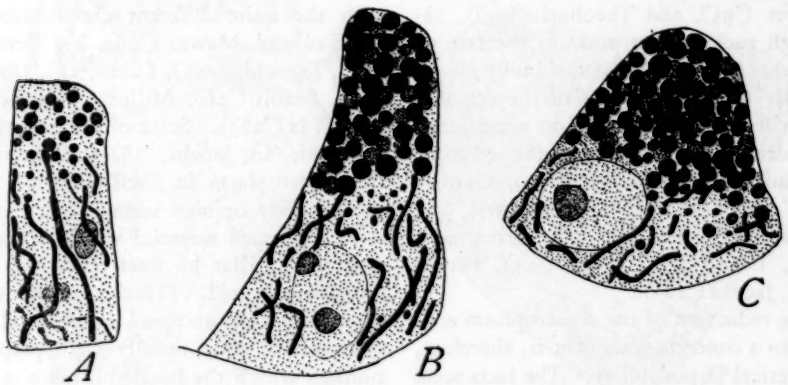

FIG. 8. STAGES IN THE SECRETORY CYCLE OF THE PANCREAS-CELL IN THE GUINEA-PIG SHOWING THE SUPPOSED DIRECT TRANSFORMATION OF CHONDRIOSOMES INTO SECRETORY GRANULES

From Hoven, 1912

Close upon the heels of the ergastoplasm theory, antedating it, indeed, in the work of Altmann, came the chondriosome theory, which for a few years achieved a remarkable vogue as an explanation of all histological differentiation. In accordance with Meves' theory, it was to be expected that chondriosomes would yield secretory granules. Indeed, as subsequently became clear, the granules (bioblasts) and 'vegetative fibers,' from which Altmann had derived secretory granules (refer to page 305), were actually chondriosomes, and thus Altmann had anticipated

many of the later developments of the chondriosome theory. Specific investigation of the problem of the relation between chondriosomes and secretory granules eventually resulted in three quite different views of the situation. According to one view, early sponsored by material was said to show a marked decline toward the end of the secretory cycle. According to the second view of the part played by the chondriome in secretion, the chondriosomes do not themselves become secretory granules, but act in some sense merely as selecting bodies or plasts

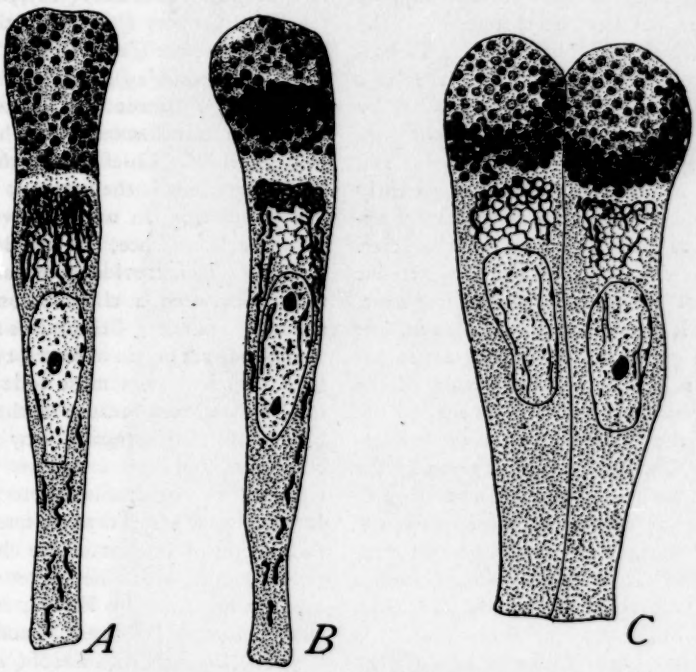

FIG. 9. RELATION OF THE CHONDRIOME TO THE 'GOLGI AREA' DURING VARIOUS STAGES OF SECRETION, IN THE STOMACH-EPITHELIUM OF THE AXOLOTL

Successive figures show the gradual consumption of the chondriosomes in the building of secretory droplets. From Tschassownikow, 1927.

Schultze ('11), and Arnold ('12), but particularly developed by Hoven ('12), Altmann's original account is corroborated. The chondriosomes in gland-cells were believed to fragment and the granules thus derived were transformed, with an accompanying increase in size, into definitive secretory droplets (fig. 8). As a necessary corollary, the amount of chondriosomal in or on which the secretory materials are deposited (fig. 7*B*). This view was particularly developed by Regaud ('09, '11) as the "eclectosome" or plast theory, and a point of view in many ways similar was also expressed by Prenant ('10) and Laguesse ('11, '24). According to Regaud the chondriosomes are the organs on which are fixed substances destined for

the chemical functioning of the cell; these organs concentrate the substances thus fixed, elaborate them and transform them into secretion-products. The third interpretation of the rôle of the chondriome in secretion is of very recent origin. Originally foreshadowed by the work of Saguchi ('20a), it has received support and more detailed development at the hands of Kull ('25), Morelle ('27), Tschassownikow ('27) and Urasov ('27, '28). It was also suggested as a possibility by Nassonov ('23), but definitely not supported by his later investigations; and Saguchi, in his original paper, apparently considered the material of the Golgi apparatus as also secretory in character. The adherents of this third viewpoint hold that the chondriosomes fragment, more or less as described by Hoven, but that the granules thus formed are subsequently modified by some action of the Golgi apparatus, becoming in the end the basis of the definitive secretory droplets (fig. 9). The details vary as given by the different authors, but the cooperation of the Golgi apparatus is, in each case, the essential feature. Here also may be mentioned the recent hypothesis of several Chinese workers (Lim and Ma ('26), Ma, Lim and Liu ('27), Ni and Lim ('28), Ma ('28b), and Ling, Liu and Lim ('28)), who believe that the chondriosomes represent a substance which is split into secretory material on one hand and Golgi apparatus on the other. This particular view is at variance with all other work on the nature of the Golgi apparatus, and to me at least seems untenable.

The view sponsored especially by Hoven has been supported in more recent years by a number of workers, for example Hauschild ('14), Schreiner ('16, '18), Beigel-Klaften ('18), Jirešová ('18), Takagi ('20, '25), Ma ('25), and Millot ('26). Of these workers, Schreiner (and also Saguchi, '20a) traces the origin of the chondriosomes to the nucleolus—a view which seems certainly incorrect, although very recently reiterated in slightly different form by Dehorne and Hosselet ('28b). Nevertheless, Hoven's interpretation has met with very serious criticism, particularly at the hands of Levi ('12), Mislawsky ('13) and Cowdry ('18); and other recent workers (Bremer ('13), Eklöf ('14), Key ('16), Calabresi ('19), Veratti ('22), Nassonov ('23), Benoit ('26)) have denied any direct transformation of chondriome into secretion. Chief among the reasons for this attitude is the fact that the staining phenomena, in which Hoven placed so much confidence, are no longer accepted as sufficient evidence of material continuity between a chondriosome and a secretory granule. I think it is fair to say that the direct origin of secretory granules from chondriosomes must today be definitely abandoned because of the impossibility of demonstrating any material continuity between a known chondriosome and a recognizable secretory droplet. It may also be added that the question of a fluctuation in amount of the chondriome synchronous with the secretory cycle, much emphasized by Hoven, is still entirely unsettled. Regaud and Mawas ('09a, b), Bremer ('13), Eklöf ('14), Grynfellt ('21), Takagi ('25), Lim and Ma ('26), Morelle ('27a), Tschassownikow ('27), and Urasov ('27, '28), corroborate Hoven's statement that there is a decline in the amount of chondriosome-material as the secretion accumulates, while Key ('16), Calabresi ('19), Nassonov ('23), Noel ('24), Jacobs ('28), and Parat ('28) deny any significant fluctuations. It is in any event a question whether any fluctuations which might occur must necessarily be given Hoven's interpretation.

Regaud's idea, on the other hand, has much to recommend it on theoretical

grounds, and has been adopted in one sense or another by several recent workers (Eklöf ('14), Calabresi ('19), Grynfellt ('21), Noel ('23, '24), Laguesse ('24), Laguesse and Debeyre ('25), and doubtfully Benoit ('26) and Ziegler ('27)). Nevertheless the demonstrable facts have not proved sufficiently positive to afford a real basis for this view and it has not achieved any wide acceptance. Its failure to win support may also doubtless be traced in part to the serious doubts which have been thrown on the chondriosomal nature of the plastids in plants, structures which were used as prototypes for the eclectosome theory.

As for the view sponsored by Saguchi, Morelle, and others, although supported by the work of several competent observers, it must be said that the derivation of secretory substances from the chondriosomes does not seem to be in harmony with most of the recent studies of the Golgi apparatus in gland-cells (cf. page 503), nor is it in harmony with the conditions in the spermatid, where the acrosomal vesicle (see beyond) develops without any morphological relation to the chondriome. And the recent work of Parat ('28) on the earliest secretory vacuoles (vacuome) offers definite and very strong evidence against the interpretation of any chondriosomal derivative as the direct forerunner of secretions.

I may add that the whole problem has been reviewed extensively by Duesberg ('12) and Cowdry ('18) who, on the basis of the older data, arrived at opposite conclusions. Their original papers should be consulted for a much more adequate statement of the problem than is possible here. See also reviews by Prenant ('10) and Eklöf ('14). In view of these very adequate discussions of the older literature I have made rather sparing reference to the older workers in the present review.

There has recently developed in the place of the earlier functional interpretation of the chondriome in morphological terms, a tendency to interpret its rôle in secretion as in the nature of an indirect contribution to some more immediate center of secretory synthesis (Bowen, '26d; Jacobs, '28; Parat, '28). It is becoming increasingly clear that only through some such indirect and largely invisible cooperation with other parts of the cell can the chondriosomes share in secretory synthesis. This view is further suggested by their distribution among the secretory droplets and other facts of similar import. However, if such a cooperative effort on the part of the chondriosomes is actually included in the direct line of secretory formation, it must be confessed that we have at present no tangible picture of the process.

The central apparatus

Amid this veritable maze of conflicting observations, of which many must certainly be incorrect, it is a pleasure to record the fact that no one has succumbed to the temptation of including the central apparatus in the list of possible organs of secretory synthesis, although its possible relation to the discharge of secretory products has been the subject of some controversy (refer, for example, to Gurwitsch ('01)). Papers like that of Gurwitsch ('01) offer the nearest approach to any possibility of secretory activity. Clearly the central apparatus may be summarily dismissed as far as its participation in secretion is concerned.

The Golgi apparatus as the focus of secretory activity

In erster Linie—und das ist das wesentlichste—treten die primären Granula als solche nur an den Maschen des Binnennetzes auf.

Nassonov, 1923.

The possibility that the Golgi apparatus might be connected with secretion is not a recent idea but dates almost from the very beginning of serious study of this structure. Negri, indeed, in 1900 studied the Golgi apparatus in the pancreas-cell and differentiated it clearly from the intracellular secretory ('excretory') capillaries, a result later corroborated by Kolster ('13), and Sundwall ('16). His remarks on this point have often been taken to mean that he expressed an opinion on the relation of the Golgi material to secretory synthesis, but a careful reading of his paper offers no basis for such a statement. Subsequently v. Bergen ('04), Kolster ('13), and Cajal ('14) considered the possible relation of the Golgi apparatus to secretion, but concluded that any morphological changes in the apparatus which might be correlated with the secretory cycle, were merely passive results of the mechanical situation within the cell. Fuchs, on the other hand, in 1902 described a "Fadenknäuel" in the cells of the epididymis which he connected with the secretory process, observing that the first secretory granules appeared within it, but not by its direct transformation. He subsequently (1904) modified this interpretation in favor of a nuclear origin of secretion; and the connection of the thread-structure with secretion was also denied by Jeleniewski ('04). There is no doubt now that the structures which Fuchs ('04) described in the cytoplasm are the Golgi apparatus, although he himself denied their equivalence to the trophospongium, a structure, the relation of which to the Golgi apparatus was at that time much discussed. Indeed, the relation of the trophospongium of Holmgren to secretory synthesis never received any very definite expression. In any event, so far as the trophospongium is actually the Golgi apparatus of other authors, the vague statements of Holmgren can not be taken as an adequate forerunner of recent views of the rôle of the Golgi apparatus in secretion. The most nearly positive statements by Holmgren connecting the trophospongium with secretion seem to be contained in his remarks on the pancreas-cell ('02b). However, the nearest approach to the modern viewpoint was undoubtedly reached by Prenant ('05), who described in certain amphibian gland-cells what he termed an "amas vermiculaire," and associated with the ergastoplasm. The secretion is first deposited in contact with the substance of this vermicular mass and Prenant says in explanation, "Il y a donc bien certainement une relation topographique et peutêtre un rapport causal entre le protoplasma différencié de cette région cellulaire et le produit de sécrétion." If one substitutes 'Golgi apparatus' for 'vermicular mass' this account would be essentially up to date. Further review of the opinions formerly expressed will be found in Nassonov ('23, '24), and Kopsch ('26), who cite a number of references here omitted.

The recent development of the subject is, however, quite original and was first made possible by the development of methods of osmic impregnation which on one hand supply incomparable demonstrations of the Golgi material itself, and on the other hand permit a simultaneous and almost perfect demonstration of the secretory products. This result is attained by first fixing the material in a fluid which is known to give a reliable fixation image (e.g., Champy), and then blackening the Golgi apparatus by proper subsequent treatment with osmic acid. In this latter operation the delicacy of the original fixation is not particularly damaged, and in many cases the secretory granules can be rendered surprisingly visible by a final staining with acid fuchsin. Such prepa-

rations of vertebrate gland-cells were first achieved by Nassonov, whose initial contribution in 1923, foreshadowed by the studies of Deineka ('16), and Kolatchev ('16), very exactly marks the origin of recent views on the subject.

In approaching the problem of a possible causal relation between Golgi apparatus and secretory granules, certain definite facts concerning the topography and distribution of the Golgi material in glandular tissue should be clearly in mind. In a general way, and avoiding the still unsolved problems of its exact structure, the Golgi apparatus seems to consist of a substance of specific type, in which lipoidal material is a conspicuous factor. In animal cells, this material occurs in the cytoplasm of gland-cells in two morphologically different forms. In one case, the material forms a tangled meshwork or platework which is often rather compact and forms a unit structure (figs. 10, 11, 12, and 16). In the other case, the Golgi material is scattered in the form of discrete pieces or 'bodies' (figs. 14, 15 and 18). Between these two extreme types there are many intergrading conditions, and the compact type is in some kinds of gland-cells regularly fragmented into Golgi bodies at a more or less definite period in the secretory cycle (lipoidal gland-cells, for example, (fig. 18); cf. Bowen ('26b)). The point is, however, that the mere morphology of the Golgi apparatus is immaterial, it is the substance itself which is of consequence (Bowen, '26d). The reasons for its assumption of such protean forms are quite unknown, but this behavior is clearly not associated primarily with con-

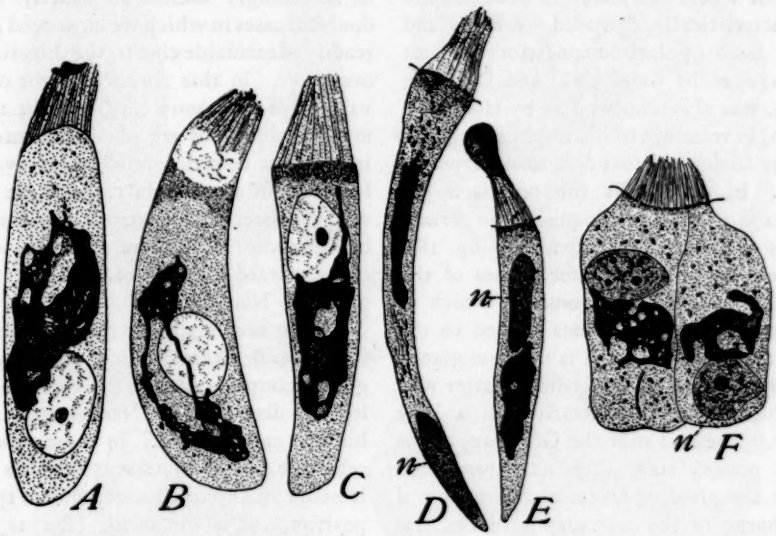

FIG. 10. RELATION BETWEEN SECRETORY POLARITY OF A GLAND-CELL AND POSITION OF THE GOLGI APPARATUS; THE GLANDULAR LUMEN LIES IN EACH CASE AT THE TOP OF THE FIGURE

A to *E*, from the cauda epididymis of the cat; *A* and *D*, normal polarity of the Golgi apparatus in 'active' and 'exhausted' cells respectively; *C* and *E*, reversed position of the Golgi apparatus in corresponding cells; *B*, intermediate position of the Golgi apparatus.—*F*, normal and reversed position of the Golgi apparatus in adjacent cells, from the vas deferens of the cat. *n*, nucleus. From Bowen, 1926.

ditions peculiar to gland-cells, since the same dispositions are met with in other types of somatic cells and in germinal tissue.

It is a general characteristic of the Golgi apparatus in gland-cells to present a rather marked polarization, in other words, to be concentrated in the zone between the nucleus (usually located in the basal region of a gland-cell) and that surface of the cell where the secretory products are characteristically extruded (figs. 10 and 11). Such a polarized condition was first emphasized by Cajal ('14) and Duesberg ('14), was also remarked on by Holmgren ('02b) in reference to his trophospongium, and is commonly found in many types of cells. In gland-cells the polarized position is regularly relinquished in certain kinds of glands (e.g., sebaceous (fig. 18), Bowen, '26b) in the later phases of the secretory cycle—a phenomenon which in many cases at least seems related to the fact that the entire cell is in these glands finally extruded. This whole matter will receive further consideration on a later page. The fact that the Golgi apparatus does present such a regular correlation with the place of origin and direction of discharge of the secretory products, has led Cowdry ('22) to suggest that the apparatus might be taken as an indicator of secretory polarity (compare also Courrier and Reiss ('22), Reiss ('22), Jasswoin ('24), Ludford and Cramer ('28)). This view was based upon the fact that in the thyroid gland of the guinea-pig, Cowdry found cases in which the apparatus was now on one side, now on the other, of the nucleus, and he interpreted this change in position as indicating the discharge of secretory material now into the cavity of an alveolus, now directly into the circulation. That the polarity of the Golgi material does coincide with the direction of the excretory current is in general certainly true, but it was pointed out by Bowen ('26c) that in a number of cases the polarity of the Golgi apparatus is reversed without any evidence of a corresponding change in the direction of excretion (fig 10). This matter has since been especially studied by Giroud ('26, '28) and Turchini ('27), and it now seems reasonably certain that the position of the Golgi apparatus is an uncertain guide, and is accordingly useless in exactly those doubtful cases in which we most need some readily identifiable clue to the direction of excretion. In this connection the observations of Nassonov ('27) on the mammalian epididymis are of unusual interest. In this case secretion-products of two different kinds are manufactured in the same cell, the direction of extrusion in one case being toward the glandular lumen, in the other toward the base of the cell. Compare also Nemiloff ('26).

Taking now a specific case to illustrate the general situation in a gland-cell, a good example is the pancreas of the axolotl as described by Nassonov ('23) in his first contribution. In these pancreas-cells the Golgi apparatus consists of a lamellar meshwork located in the typical position for a gland-cell (fig. 11). In the earlier phases of the cycle the secretory granules all lie within the general area enclosed by the Golgi network, where they are easily visible as yellowish spheres, or, after staining with acid fuchsin, as conspicuous red granules. In the majority of gland-cells in vertebrates, this area would obviously correspond to the region close to the nucleus and on the side toward the glandular lumen (fig. 10), and this region has often been noted as the place of first appearance of secretory droplets by workers most of whom had no intimation of the presence of the Golgi apparatus (cf. Leydig ('57), Bensley ('98), Maximow ('01), Schmincke ('03), Ar-

nold ('05), Weiss ('09), Key ('16), Saguchi ('20a, the 'secretogenous area'), etc.) As the production of granules proceeds, the Golgi area, by which I mean merely to denote the space roughly included by the peripheral limits of the Golgi material, sometimes becomes gorged with secretion, like a basket filled with cherries (fig. 11*A*). Eventually the granules begin to move away and collect in the area of the cell next the glandular lumen (figs. 11*B* and *C*).

An equally good example, of a slightly different type, is the goblet cells of the intestine in Amphibia (Nassonov, '23; Bowen, '24a). Here the Golgi network is disposed like a long cylindrical meshwork in the area just distal to the nucleus (fig. 12). This becomes filled with secretory droplets which gradually migrate out to build up the familiar 'goblet,' and in the final stages the whole Golgi apparatus collapses (Bowen, '24a) as though to express the remaining secretory products, as the contents of the goblet are made ready for release. The fact is thus clearly established that an intimate topographical relationship exists between the Golgi material on one hand and secretory products on the other. The first step in the analysis of the situation thus presented is obviously to make an extended examination

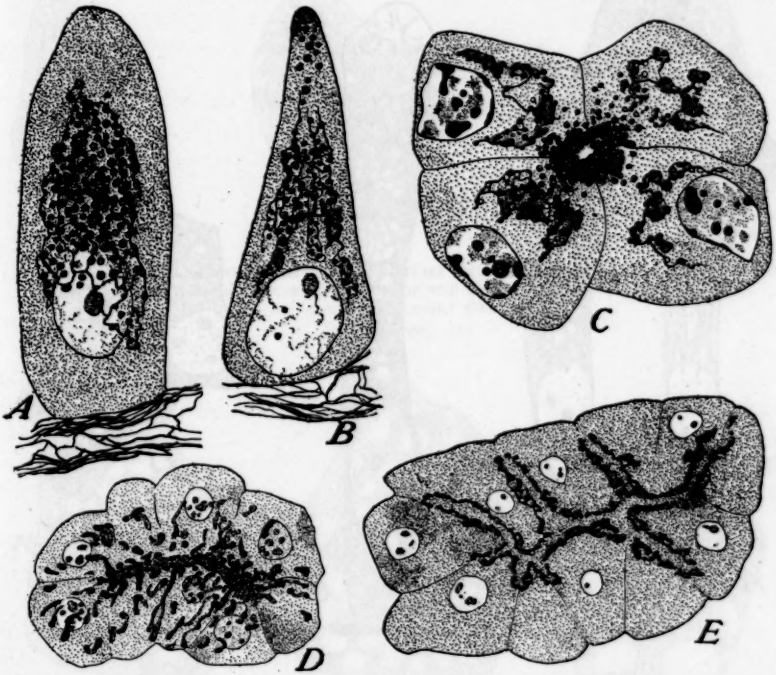

FIG. 11. THE GOLGI APPARATUS IN RELATION TO SECRETORY ACTIVITY IN THE PANCREAS

A to *C*, from the axolotl; *D*, *E*, from the mouse, three hours after injection of pilocarpine—*D*, stained by the Kull method, to show the chondriosomes and the appearance of new, as yet very small, secretory granules along the border of the glandular lumen; *E*, similar cells prepared to show the Golgi apparatus, for comparison with *D*. From Nassonov, 1923 and 1924.

of glandular tissues to ascertain whether topographical relations of the same type everywhere obtain. If there is any causal relation between the Golgi material and the origin of secretion-droplets, one might then expect to find an intimate and invariable topographical relation. The facts have now been examined in a considerable variety of gland-cells, a partial tabulation being given by Jacobs ('27), and on the basis of this evidence Bowen ('26d) has pointed out that there are certain rather obvious differences in the topographical details, which may be shown often to correspond in a rough way with the type of gland-cell. The simplest arrangement is that which occurs in the goblet-cells, described above, and likewise in salivary glands of the mucous type (Bowen, '26a), lachrymal glands (Bowen, '26c), glands of the male reproductive tract (Bowen, '26c; Nassonov, '27; Parat, '28), etc. In these cases, the secretory droplets clearly have their origin within the Golgi area, but are rapidly completed and move away toward the glandular lumen to be stored until occasion arises for their extrusion (fig. 12). In some gland-cells of this type the stored products may apparently be extruded in part at least

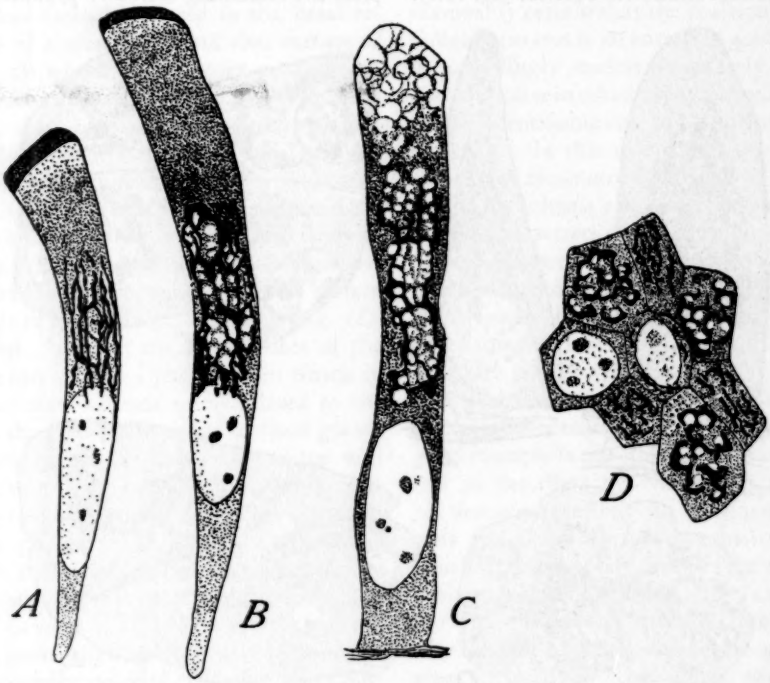

FIG. 12. THE GOLGI APPARATUS IN RELATION TO SECRETORY ACTIVITY IN CELLS OF THE INTESTINAL EPITHELIUM OF TRITON

A to *C*, steps in the formation of the characteristic 'goblet' at the free end of the cell; *D*, cross-section of cells in various phases of the secretory cycle. The secretory droplets appear as clear unstained vacuoles. From Nassonov, 1923.

without any essential disturbance of the active zone of secretory synthesis. Thus a continuous secretion-stream pours slowly out of the Golgi area, proceeding, after a longer or shorter pause, on out of the cell into the lumen of the gland.

phenomenon was clearly described by Altmann ('94) in the parotid of the cat, and has since been noted by several other workers (e.g., Bowen, '26a). While there is reason to believe that the maturing of the granules may be quite independent of

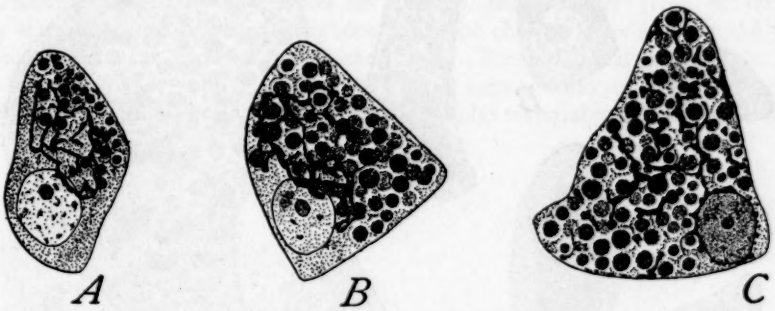

FIG. 13. THE GOLGI APPARATUS IN RELATION TO SECRETORY ACTIVITY IN THE PAROTID GLAND OF THE CAT, SHOWING THE PROGRESSIVE EXTENSION OF THE GOLGI NETWORK THROUGHOUT THE MASS OF SECRETORY DROPLETS
From Bowen, 1926

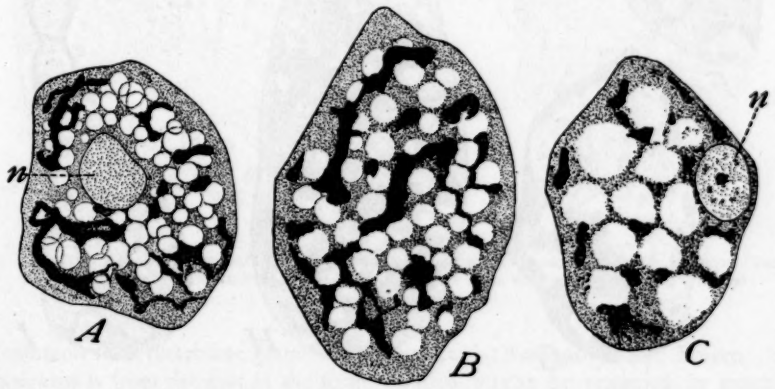

FIG. 14. STAGES IN THE SECRETION OF LIPOIDAL MATERIAL IN THE WHITE PORTION OF THE INGUINAL GLAND OF THE RABBIT

A, *B*, earlier phases in the production of lipoidal droplets; *C*, later stage of fusion of droplets, with accompanying disintegration of the Golgi material. *n*, nucleus. From Bowen, 1926.

In other kinds of glands, however, the granules seem to require a longer period for their production, involving a process of 'maturing' which affects all of the secretory droplets simultaneously. This

the Golgi apparatus, nevertheless the synthesis, by more or less simultaneous growth, of a whole batch of secretory granules, introduces a complicating factor. This situation seems to be met by

the expedient of extending the Golgi material in all directions through the mass of secretory products, close topographical relations being thus retained throughout the period of development (fig. 13). Such

The same end might, likewise, be accomplished by distributing the Golgi material throughout the mass in the form of scattered pieces. This is actually what happens in another group of cases, the

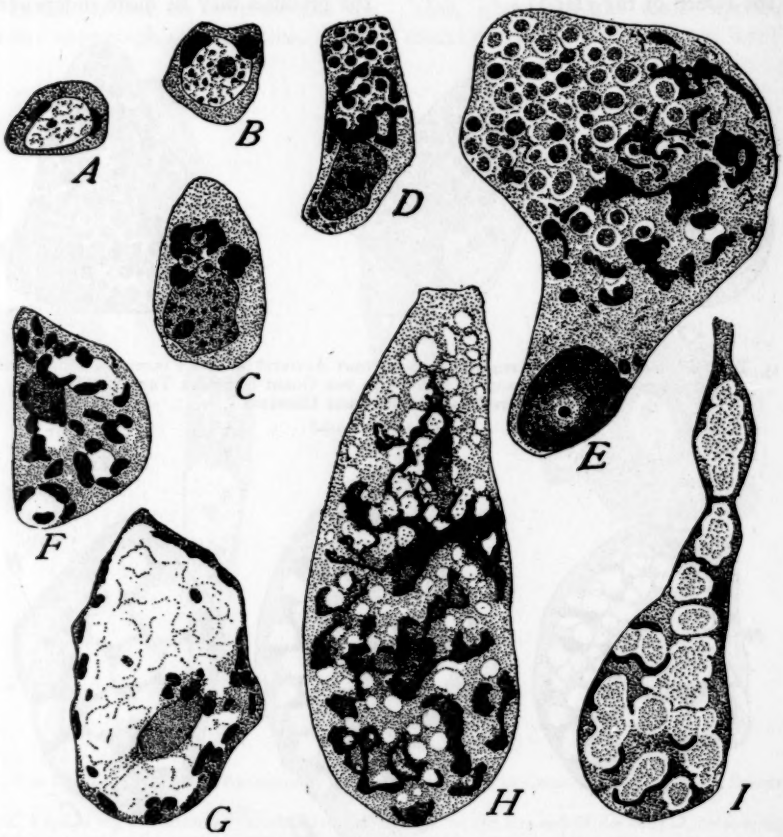

FIG. 15. SCATTERED CONDITION OF THE GOLGI APPARATUS—GOLGI BODIES—FREQUENTLY FOUND IN THE GLAND-CELLS OF INVERTEBRATES

A to *E*, progressive stages in the secretory cycle of a serous cell from the salivary gland of *Limax; F, G*, earlier and later stages respectively of mucous cells from the salivary gland of *Limax;* from Bowen, 1926.—*H, I*, deep-lying mucous cells in *Hirudo;* from Nassonova, 1927.

is the condition in the parotid gland of the cat, where the apparatus gradually loses its initial, rather compact form, and insinuates itself in all directions among the developing granules (Bowen, '26a).

result being attained in two slightly different ways. In one type, represented by the so-called 'skin-glands,' which produce lipoidal secretions, the apparatus is at first compact, but very early in the se-

cretory cycle it begins to fragment, and the products, in larger (inguinal gland of the rabbit (Bowen, '26b), and mammary glands (Da Fano, '22); (fig. 14)), or smaller (avian oil glands, Meibomian, sebaceous, and Harderian glands (Bowen, '26b; Ludford, 25), (fig. 18)) pieces become scattered more or less throughout the secretory mass, depending on the method of extrusion which happens to obtain in the particular case. In another type, common in invertebrate gland-cells, the apparatus is from the first in the form of discrete Golgi bodies which become widely scattered among the developing secretory granules (fig. 15). In some of these cases more or less fusion of the droplets is known to occur in the later stages, and this suggests that a similar process might be one way in which large granules could be produced at points removed from direct topographical relations with the Golgi apparatus.

One further type of association between secretory granules and the Golgi material remains to be mentioned, although in my own opinion the validity of the interpretation is not yet above suspicion. The situation occurs in some gland-cells in which the granules grow or undergo marked changes after leaving the Golgi area. The individual granules in these cases seem to carry away a small portion of Golgi material in the form of a 'girdle' or 'cap' (Nassonov, '23; Bowen, '24a), which might be regarded in much the same light as the case of the scattered Golgi bodies previously described (fig. 16). Unfortunately, the occurrence of somewhat similar structural peculiarities in cases where the presence of Golgi material would appear not to be a satisfactory explanation, suggests that a final conclusion be deferred until a more extended and critical examination of this situation can be made.

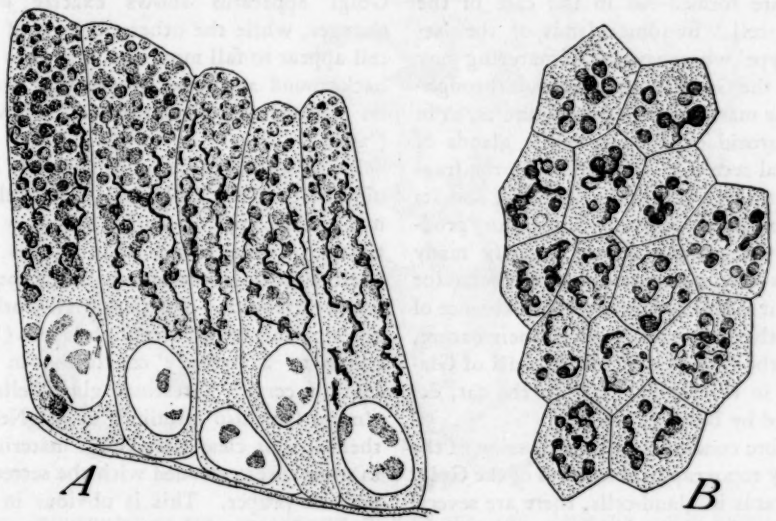

FIG. 16. LONGITUDINAL AND CROSS-SECTIONS OF CELLS FROM THE PELVIC GLAND OF TRITON, SHOWING RELATION OF THE SECRETORY DROPLETS TO THE GOLGI NETWORK AND TO THE OSMIOPHILIC GIRDLES
From Nassonov, 1923

If one now considers the general types of behavior presented by the Golgi apparatus in gland-cells of different kinds, he will be struck by an obvious, if rough, correlation with the old histological classification of glands. Thus, Bowen ('26d) has pointed out that in gland-cells of the 'mucous type,' the apparatus tends to maintain a rather fixed relation to the zone of developing granules, the granules themselves moving quickly away as rapidly as they are formed—as in the case of the goblet-cell. In some glands of the 'serous type' where a period of maturing may occur, the Golgi material spreads throughout the mass of developing granules, as in the parotid of the cat; while glands of lipoidal secretion are marked by the fragmentation of the Golgi material and its distribution throughout the secretory product. One might indeed classify many glands from a knowledge of the behavior of their Golgi apparatus, in the absence of any other information as to their nature, as in the case of the crescent-cells of Gianuzzi in the submaxillary of the cat, described by Bowen ('26a).

Before concluding this discussion of the purely topographical features of the Golgi apparatus in gland-cells, there are several associated points which should be emphasized.

In the first place, it is important to note that during the secretory cycle the Golgi apparatus undergoes a marked hypertrophy. This was first pointed out clearly by Cajal ('14), who came very close to the view of the Golgi apparatus which was later suggested by Nassonov. It is, however, to be particularly noticed that this increase in the amount of Golgi material is related to the volume of the secretion-product rather than the undifferentiated cytoplasmic background or the nucleus—both of which may appear actually to decrease in size as the secretory cycle progresses. When it is further considered that the chondriosomes have been said by some (page 489) to decrease during secretion, the significance of the hypertrophied Golgi material may be more apparent. If it is reasonable to suppose that the elements involved in secretory activity would show changes in the direction of increased activity as expressed in size-increase and change in morphology, then it seems significant that the Golgi apparatus shows exactly such changes, while the other elements of the cell appear to fall more and more into the background as the secretory cycle draws on toward its conclusion (cf. Bowen ('26d)).

In the second place, it is indirectly significant that the Golgi material itself is not visibly used up during secretory activity, in other words that it does not itself seem to be transformed into the secretory granules. Practically all workers agree on this point, although Jacobs ('28) comes to a contrary conclusion in the case of certain intestinal gland-cells in *Astacus* (see also Nemiloff('26)). Nevertheless, it is clear that Golgi material is in some cases extruded with the secretory product proper. This is obvious in the case of glands of the holocrine type (the inguinal gland of the rabbit is a good example, Bowen, '26b), and may very likely occur to some extent in any gland-cell from which there is a very extensive excretion at any one time. It is also worthy of note, that Golgi pieces can sometimes be demonstrated among the extruded secretion-products (fig. 17), thus indicating that it possesses a distinct, material reality which is retained even after leaving its normal cellular location (cf. Brambell ('25), Bowen ('26b), Beams ('27)). Brambell ('25) believes that in the secretory cells in the oviduct of the hen, the Golgi material is entirely cast out of the cell to-

gether with the secretion proper, to be reconstituted de novo for the next secretory cycle. Other workers who have particularly examined early phases in the secretory cycle, of which the pancreas-cell in the mouse as described by Nassonov ('24) offers an especially good example (fig. 11 *E*), have, however, failed to corroborate this account. It seems certain, therefore, that merocrine gland-cells usually retain part of the Golgi material, which, after sharing in the necessary reorganization which may mark the close of a secretory cycle, is retained as the definitive Golgi material.

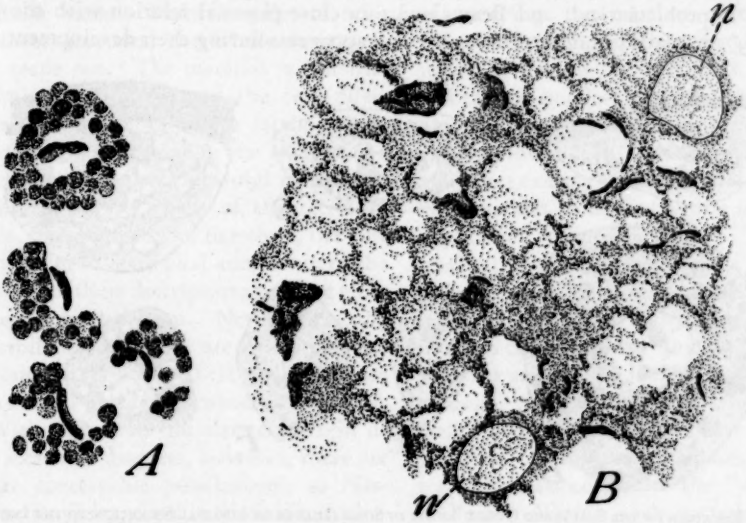

FIG. 17. MAINTENANCE OF THE CHARACTERISTIC FORM OF THE GOLGI APPARATUS (GOLGI BODIES) AFTER BREAKDOWN OF THE CELLS IN WHICH THE APPARATUS WAS ORIGINALLY CONTAINED

A, secretory granules and Golgi bodies from the oil-gland of the duck; *B*, secretory mass with contained Golgi bodies after disintegration of the cells in the red portion of the Harderian gland of the rabbit. *n*, nucleus. From Bowen, 1926.

It is thus evident that in a very long series of gland-cells, in both vertebrates and invertebrates, the fact has been established that there is a constant topographical relation between Golgi apparatus and secretion-products in process of formation, the Golgi area marking, indeed, the invariable focus where secretory droplets make their initial appearance. This topographical interrelation has been dealt with by Nassonov ('23, '24, '26, '27), Bowen ('24a, '26a, b, c, d), Jasswoin ('25), Kopsch ('25, '26), Ludford ('25a, b), Cramer and Ludford ('26a, b), von Lanz ('26), Nemiloff ('26), Beams ('27), Morelle ('27a), Nassonova ('27), Tschassownikow ('27), Urasov ('27), Ludford and Cramer ('28), and Parat ('28); reference should also be made to Cramer and Ludford ('25), and Weiner ('28) on fat-absorption in the intestinal cells. A general discussion of the topographical situation is given by Nath ('26) and Jacobs ('27). Not only is there a mere spatial relation between secretory products and Golgi material, but the latter has been shown to assume various types of arrangement correlated with the kind of secretion that is being synthesized. Of all the cellular constituents, it is the Golgi

apparatus alone which seems to present morphological features peculiarly connected with secretory phenomena within the cell. Such a close spatial interrelation is a prime necessity of Nassonov's theory, and it is worthy of peculiar emphasis that no one has yet found a case where these topographical considerations could be denied, except perhaps in certain cases described by Chlopin ('27), the exact relation of which to the Golgi apparatus is problematical, and Beams and Wu ('29) on insect spinning glands.

Golgi material is still relatively little understood. Indeed, recent comment on this particular phase of the Golgi-problem has served only to increase rather than decrease the difficulties of interpretation (e.g., Bowen ('24a, '26b, '27), Hirschler ('27), Parat ('28), and Morelle ('27a and b)). From a morphological point of view the appearances suggest that the secretory vacuoles arise de novo within, or on the surface of, the Golgi material, and remain in close physical relation with the Golgi apparatus during their development. Un-

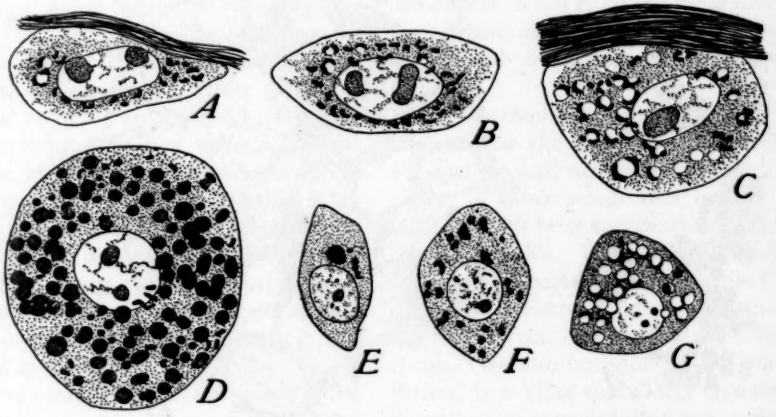

FIG. 18. RELATION OF THE SCATTERED GOLGI BODIES IN SOME GLANDS OF LIPOIDAL SECRETION TO THE INDIVIDUAL SECRETORY DROPLETS

A to *D*, progressive stages in sebaceous glands of the mouse. From Ludford, 1925.—*E*, earliest, condensed condition, and *F*, later scattered condition of the Golgi apparatus in the oil-gland of the common fowl; *G*, later phase of the same, showing intermediate stage in the production of fatty droplets. From Bowen, 1926.

The general topographical interdependence of Golgi apparatus and secretory granules having been thus established with reasonable certainty, the problem remains as to the more exact relation of individual secretory granules to the Golgi material. In exactly what terms can we picture this relation from a standpoint not only morphological but physiological as well. Certain aspects of this problem are as yet entirely obscure, owing to the fact that the intimate structure of the

fortunately, in practically all cases, the number of secretory granules present in a single cell is so great, and the exact limits of the Golgi apparatus so ill-defined, that a clear-cut picture of the exact nature of the relation is difficult to obtain. The figures of the amphibian goblet-cell given by Nassonov ('23) are perhaps as suggestively clear as any (fig. 12). There is, however, one case in which the topographical relationship seems remarkably definite. This is in certain gland-cells

producing lipoidal secretions. Ludford ('25b) in sebaceous glands of the mouse and Bowen ('26b) in the oil gland of the fowl, independently observed that the fragments of the Golgi apparatus, characteristically formed in such glands, are associated with specific, individual, secretory droplets (fig. 18). In such a case, each granule seems to be associated with a small piece of Golgi material, and the topographical situation is reduced to its ultimate terms. Unfortunately, in both of these accounts, the whole story was not made out. The material is, further, technically difficult, and the case offers some other features which might justify another interpretation in the absence of a complete account of the Golgi material in absolutely every phase of the secretory cycle. It seems to me, therefore, the part of wisdom to defer final acceptance of the validity of these descriptions pending more adequate examination. Nevertheless, the possibilities suggested are of critical importance and offer the best present chance of a crucial proof of Nassonov's theory.

With respect to the ultimate origin of the secretory droplets, however, there are other conceivable possibilities, as Nassonov ('23) suggested in his first contribution. For example, the original granules might be derived from the fragmentation-products of mitochondria or from some ultimate protoplasmic particles like Heidenhain's 'protomeres.' Nassonov himself has never attempted to develop these suggestions into the status of probabilities, and the great majority of workers have not found any evidence to support the view that the beginnings of secretory granules are found in chondriosomes or other definite particles of the cytoplasm. However, certain workers (see page 321), have considered mitochondria as the source from which comes the material worked upon by the Golgi apparatus. But I think it fair to conclude that the weight of evidence is in favor of viewing the earliest secretory vacuoles as structures not to be traced to any direct morphological relation with cellular structures previously present in the cell.

The very recent work of Benoit ('26), Hirschler and Hirschlerowa ('28), and Parat ('28) and his colleagues has thrown a great deal of light upon this whole problem of secretory beginnings. The difficulty of studying the relation of the individual secretory droplet to the Golgi substance is due to the fact that the very earliest and smallest secretory droplets are not well demonstrated by the usual technical methods. Parat has shown, however, that exactly these stages in secretory synthesis can be stained by the intra-vital application of neutral red. The very smallest droplets or vacuoles are thus brought clearly to view, and the whole story of their transformation into secretory droplets can be traced. It is clear that the vacuoles arise in the Golgi area, probably through its activity, and thus is furnished a constant source of new secretory vacuoles. These earliest phases of secretory synthesis constitute the "vacuome" of Parat. Within each vacuole appears the segregation granule (of Renaut, p. 307), which itself is not usually stainable by neutral red but can be demonstrated after fixation, by acid fuchsin. As the secretory droplet grows to maturity, its capacity for staining with neutral red disappears coincidently with the filling up of the enclosing vacuole. As Benoit ('26) has clearly pointed out, although Parat ('28) himself offers a rather different interpretation, (see page 507), the topographical relation of the vacuome,—i.e., the primordial secretory droplets,—and the Golgi apparatus leads to the conclusion that the vacuoles originally appear embedded in or on the Golgi material, and

subsequently become free as recognizable secretory droplets (fig. 19*A*). And this conclusion is supported by many of the results of osmic impregnation, in which the vacuolated appearances of the Golgi material were for some time a source of difficulty (e.g., Bowen, '26c).

The problem remains as to the nature of the physiological relation possibly existing between the Golgi material on one hand and the contents of a secretory vacuole on the other. There is obviously no direct evidence as yet which bears on this point, but two possibilities are more or less implicit in published work. Of these, Nassonov ('26) in particular regards the Golgi apparatus as active only in the elective concentration of the secretory materials, which are themselves primarily the product of chemical synthesis in the general protoplasm. The other view, which I have myself held in rather indefinite form, considers the Golgi apparatus as taking some active part in the synthesis of the final secretion-product. The evidence now at hand can scarcely be said to warrant any particularly decided opinions on the point in question.

There is, however, another source of extraordinarily interesting data bearing on the problem both morphologically and physiologically—namely, the relation between the Golgi apparatus and the secretion of so-called vital dyes. As is well known from the researches of Möllendorff, vital dyes behave toward protoplasm in two quite different ways according as the dye is acid or basic. Basic dyes enter cells without difficulty and are deposited in (in other words, stain) bodies such as chondriosomes (in the case of janus green) or vacuoles (in the case of neutral red), which had a perfectly definite preexistence in the cell. Acid dyes, on the contrary, enter relatively few kinds of cells, which must in addition be in their proper

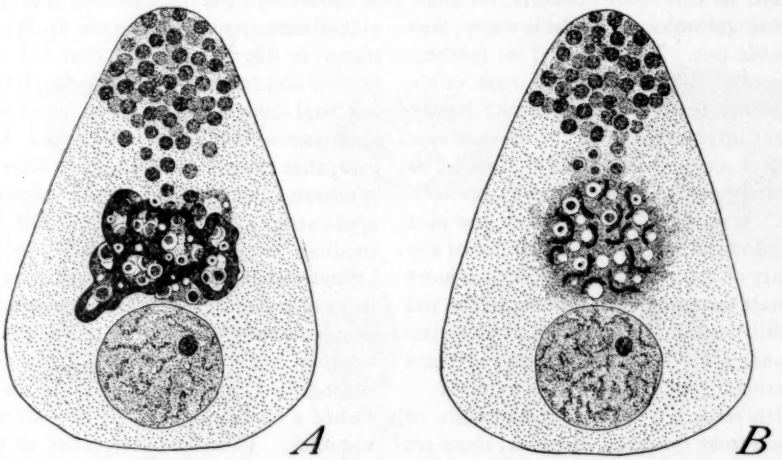

FIG. 19. SCHEMATIZED REPRESENTATION OF THE TWO VIEWS OF THE ARCHITECTURE OF THE SECRETOGENOUS AREA IN A GLAND-CELL

A, the Golgi apparatus and its relation to the secretory droplets, according to Bowen and others. *B*, the secretory droplets (in their earlier phases, the vacuome) and their relation to the "diffuse lipoids" (more heavily stippled area) and "active chondriome" (black, rod-like bodies in the area of diffuse lipoids) of the secretogenous area, according to Parat, 1928.

place in the living body. But in such cases, the dye is deposited not in preformed elements of the cytoplasm, but in new formations (vacuoles) which are part and parcel of the reaction of the cell to the dye. In other words, acid dyes are 'secreted' within the cell in a manner which, morphologically at least, recalls some of the characteristic features of normal secretory phenomena. If the production of a secretory granule is thus in a sense comparable to the formation of a granule of a soluble vital dye, one may suppose that the action of the cellular mechanism is in the two cases similar in at least some respects. We should expect, therefore, under these possible circumstances, to find that the secreted granules of vital dyes bear the same topographical relations to the Golgi apparatus as the true secretory granules.

The possibilities of such histophysiological examination have now been rather adequately investigated, and the actual results have borne out in a most amazing manner the theoretical expectation. The first results were published by Jasswoin ('25) on the kidney-cells of Amphibia. These were soon amplified by Nassonov ('26) on the kidney of the axolotl, the white mouse, and the cat, the liver of the mouse and of *Lacerta*, and in a subsequent paper ('27), the epididymis of the rabbit and guinea-pig. Similar contributions have been made by Makarov ('26), Glasunow ('28), and Ludford ('28); and the suggestive experiments of Chlopin ('27) with neutral red, in the production of his so-called 'Krinome,' and the recent study of Rumjantzew ('28), should also be mentioned. All of the workers who have experimented with trypan blue concur in the conclusion that the distribution of the first-formed granules of the dye corre-

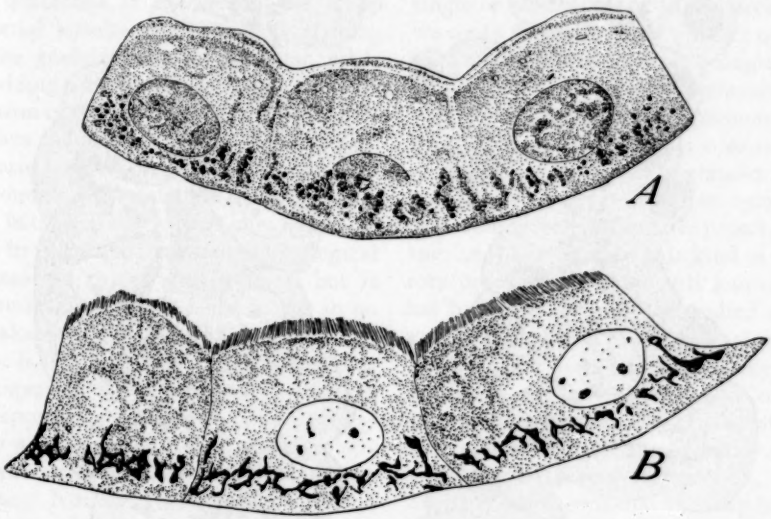

FIG. 20. RELATION OF THE GOLGI APPARATUS TO THE ACCUMULATION (SECRETION) OF A VITAL DYE (TRYPAN BLUE) IN THE KIDNEY-CELLS OF TRITON

A, the distribution of the vital dye; *B*, complementary preparation to show the corresponding topography of the Golgi apparatus. From Jasswoin, 1925.

sponds exactly with that of the Golgi apparatus. These results should be compared with Peter ('24) and with many of Möllendorff's figures, and also with the old observations of Krause ('01) and others of similar nature, which quite unknowingly demonstrated the topographical sequence.

neys, cells are found with granules of the dye distributed in a corresponding way (fig. 20 *A*). Perhaps the most striking case of all is that furnished by the liver of *Lacerta* (Nassonov, '26), where the Golgi apparatus has a very unusual distribution adjacent to the bile capillaries (fig. 21*B*).

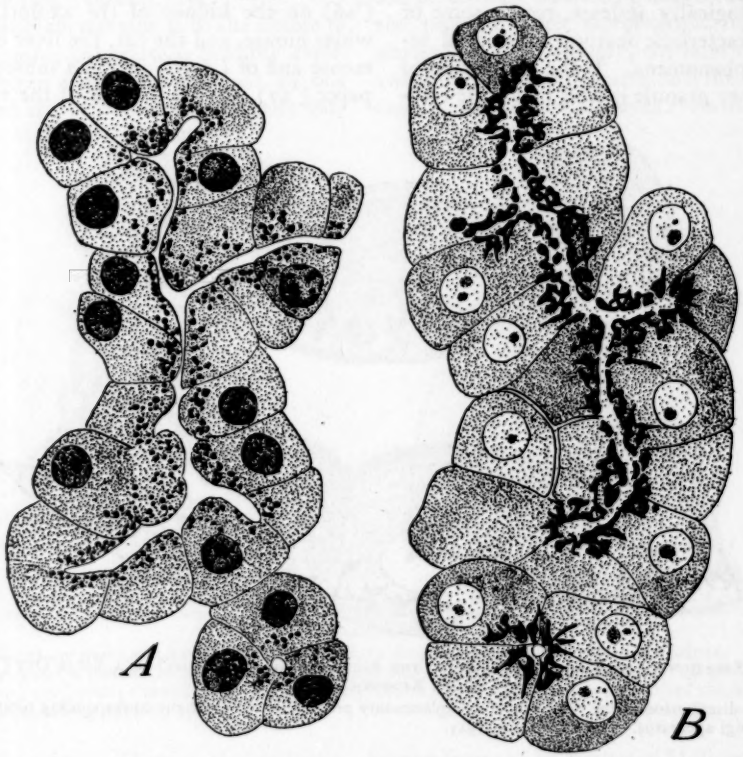

FIG. 21. RELATION OF THE GOLGI APPARATUS TO THE SECRETION OF A VITAL DYE (TRYPAN BLUE), IN LIVER-CELLS OF LACERTA
A, *B*, like fig. 20. From Nassonov, 1926

perposition of the granules of 'secreted' vital dyes on the Golgi apparatus. Thus in the kidney of *Triton* in certain cells Jasswoin showed that the Golgi apparatus had a rather striking distribution—basal to the nucleus (fig. 20 *B*). Similar animals are now given injections of trypan blue, and upon examination of the kid-

Trypan blue injections result in the appearance of blue granules in the same position in the cell (fig. 21*A*). It is thus demonstrated beyond doubt that the cellular zone in which acid dyes are 'secreted' corresponds to the Golgi area, and that the dye-granules are never seen in any other part of the cell during the earlier

phases of their production. Nassonov and Jasswoin were unable to impregnate the Golgi apparatus and still retain the natural coloring in the granules of vital dye. Their demonstration, while convincing, was thus lacking in one point which is of particular interest in view of the recent assertions of Parat ('28) as to the homology of vacuoles and the classical Golgi apparatus. This missing link has now been supplied by Ludford ('28), who has succeeded in blackening the Golgi material simultaneously with a staining of the granules of vital dye, the whole providing a remarkably conclusive demonstration of Nassonov's theory.

Thus the problem stands at the present moment. It is perhaps unnecessary yet to commit one's self finally to the view that in the activity of the Golgi apparatus is to be found the long-sought cytological explanation of secretory origins; but it is nevertheless proper to point out in no mistakable terms that Nassonov's account is the only view of the matter thus far expressed which has seemed to have any appearance of that universal applicability which any solution of the cytological problem of secretion must indubitably possess. Not only with respect to the purely morphological features, but in such physiological experiments as have thus far been possible, the fragments of evidence seem to fit logically into a single unified conception of the cytology of glandular secretion.

But, as I have elsewhere remarked, it is one thing to note certain obvious relations existing in a general way between the Golgi apparatus and a mass of secretory granules and to conclude therefrom that the Golgi apparatus produces the granules; it is quite another thing to reduce this relation to the critical case of a single granule and thus to arrive at some real conception of how secretory products are actually related to the Golgi substance. It remains now to inquire whether there is any further light to be thrown on this difficult point from some hitherto unsuspected angle.

It will, I think, be evident that the matter in question, like the whole problem of secretory origins, is made difficult primarily by the fact that secretory granules are present in a given cell in such large numbers that it is impossible to study any single or particular one in any detail. If we could find a secretory product of some kind which was produced as a single granule, or at most a very few granules, we could obviously study the phenomena of both origin and growth in a manner quite impossible in an ordinary gland-cell. It was pointed out by Bowen in 1923 (and more fully developed in later papers, '24a, and '26d) that exactly this kind of secretory product is already well known and has been very thoroughly studied as the so-called acrosome of the animal sperm. This structure has, to be sure, long been considered as a 'cutting-tool' modeled during sperm-formation out of almost any material that happened to be handy. But in a series of papers Bowen ('22, '24b, '25, etc.) has shown that this hap-hazard derivation of the acrosome is entirely a product of inadequate technique and inaccurate observation. The acrosome actually is a substance which is produced invariably in association with the Golgi apparatus of the spermatid. To put a long story into a few words, it is now perfectly clear that the acrosome is somehow a product of the activity of the Golgi apparatus, but that in its production the substance of the Golgi apparatus is not directly transformed into acrosomal material. When the acrosomal material has been produced, the Golgi apparatus is still present substantially as at the beginning of the process and is finally (in most

cases) cast out of the sperm, like a useless remnant, together with other detritus of spermatogenesis. These waste materials together constitute the protoplasmic balls, the casting off of which from the nearly completed sperms is a process at once well known and characteristic. This history is in essence the cytological story of the production of a secretion-product, and the paratus, but morphologically it often presents the differentiation into a vacuole and an enclosed granule which is so obvious a characteristic of many secretory droplets (figs. 1 and 22 *B*). Thus Bowen suggests that from the standpoint of acrosome-formation, light is shed upon the details of the mode of origin and growth of secretory droplets, and that from the stand-

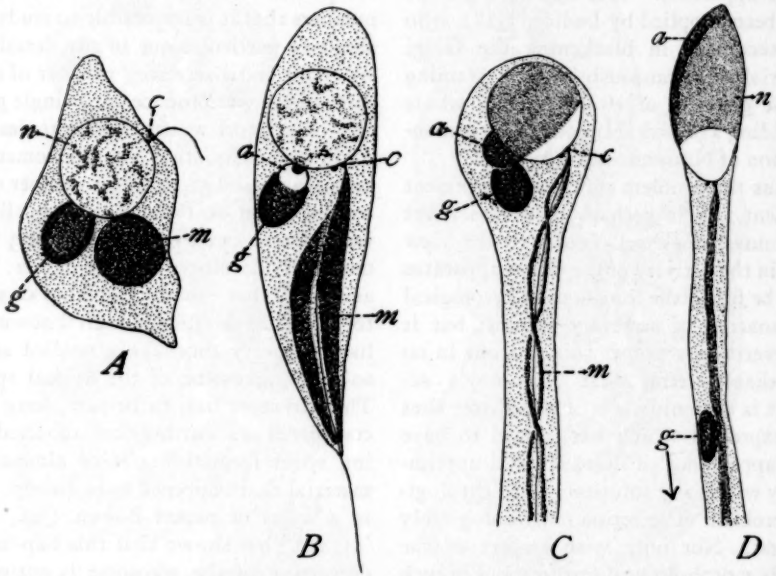

FIG. 22. THE RELATION OF THE GOLGI APPARATUS TO THE FORMATION OF THE ACROSOME IN THE ANIMAL-SPERM; SCHEMATIZED FIGURES BASED ON THE CONDITIONS IN HEMIPTERA, ACCORDING TO BOWEN

A, early spermatid prior to the appearance of any acrosomal material; *B*, formation of the acrosome; C, separation of the Golgi apparatus from the acrosome; *D*, application of the acrosome to the developing sperm-head (nucleus) and retreat of the Golgi apparatus down the tail of the sperm. *a*, acrosome; *c*, centioles and related axial filament; *g*, Golgi apparatus; *m*, chondriosomal body or nebenkern; *n*, nucleus.

only question which can well be entertained about it, is whether this secretion, the acrosome, can be in any way compared with a glandular secretion, the zymogen granules, for example. Bowen believes that the evidence points unmistakably to the essential similarity of the acrosome with an ordinary secretion-granule. Not only does the acrosome present the same topographical relations to the Golgi apparatus, but morphologically it often presents the differentiation into a vacuole and an enclosed granule which is so obvious a characteristic of many secretory droplets (figs. 1 and 22 *B*). Thus Bowen suggests that from the standpoint of acrosome-formation, light is shed upon the details of the mode of origin and growth of secretory droplets, and that from the standpoint of the gland-cell, light is shed upon the real significance and function of the acrosome. He concludes therefore, with the suggestion that the acrosome is a secretory product pure and simple, the function of which is to set off the fertilization-reaction. Fuller statements of the views here outlined together with actual details of acrosomal behavior, will be found in Bowen ('22a, b, '26d, etc.).

The morphology of acrosome-formation becomes thus unexpectedly of prime importance to a more detailed understanding of secretory synthesis. The production of acrosomal material is subject to many variations in detail, but the essential points are well illustrated by Hemiptera of the family Pentatomidae. In these forms (Bowen, '22a), the earliest spermatid contains a number of scattered Golgi bodies which, by successive fusions, finally combine to form a single, thimble-shaped mass (fig. 22 *A*). The 'opening' of the thimble is turned toward, and is in contact with, the nuclear membrane. Presently there appears at the mouth of this thimble a small, clear vacuole (fig. 22 *B*), which gradually grows larger as the earlier phases in the transformation of the spermatid are progressing. Within this vesicle a characteristic granule (segregation granule?) presently appears. When this complex of vacuole and granule has been completed, the Golgi apparatus breaks away (fig. 22 *C*) and travels backward along the sperm tail—an apparently useless remnant (fig. 22 *D*). The acrosomal material, on the other hand, migrates around the nucleus and presently begins the series of morphological changes which finally result in the acrosome of the mature sperm (fig. 22 *D*).

We have thus, in the production of the acrosome, a large-scale simulacrum of the production of each secretory granule in a gland-cell, and the probable morphological relationship of Golgi material to secretory product is made transparently clear. Bowen himself did not extend his observations to living cells, but this final step in the evidence which would link together the acrosome and secretory granules as essentially expressions of a single phenomenon (secretion) has been recently completed by Parat ('28) and particularly by Hirschler and his pupils, and Gatenby ('29). Parat's work was partly done in collaboration with several of his students, and a bibliography will be found in the reference cited; of the papers from Hirschler's laboratory note particularly Hirschler ('28), Hirschler and Monné ('28). These workers have shown that in many cases the developing acrosome, sometimes the proacrosomal material also, responds to neutral-red staining in much the same way as true secretory vacuoles.

Concerning the physiology of acrosome-formation we know nothing as yet, but it is perhaps worth while to observe that the condition of the spermatid-chondriosomes, condensed as they are into the compact 'nebenkern,' permits a conclusive demonstration of the fact that the chondriome does not share in any direct (morphological) way in the synthesis of the acrosome (fig. 22 *B*), as the theory of Saguchi, Morelle, and others (see page 490) would seem to require. With respect to the physiological interpretation of the acrosome, and its function in the egg, as suggested by Bowen's hypothesis, it is interesting to note that Hibbard ('27) has recently brought forward evidence of the presence of an enzyme in the acrosome of the *Discoglossus*-sperm. This is the first positive indication that the interpretation of the acrosome as a secretion is correct. The older experiments of Goodrich ('20) on the behavior of the *Nereis*-egg from which the sperm had been removed by micromethods as soon as was possible after it (the acrosome?) had touched the egg, should also be taken into consideration here. This aspect of the situation is more fully discussed by Bowen ('25).

Whatever, therefore, the final judgment on Nassonov's theory may prove to be, it is even now impossible to avoid the conclusion that in some cases at least the Golgi apparatus is directly concerned in the production of secretions. Not least

important in this conclusion is the fact that for the first time we have a conception of the secretory process which brings under one common viewpoint a series of hitherto unrelated phenomena—phenomena, indeed, whose possible relations to each other were not even suspected. Exactly how the Golgi apparatus operates we do not know, except that there is reason to believe that it does not function as an independent cell-organ. Secretory activity seems rather to be a function in which the whole cell-system is somehow involved, presumably in the sense that it cooperates in providing the raw or finished materials which are to be deposited in the secretory vacuoles. This point has recently been again emphasized by Jacobs ('28) (see also Ludford ('25a), Bowen ('26d), Tschassownikow ('27), Ma ('28a), Parat ('28)). In such a scheme of things, the nucleus and chondriosomes may well have some definite share and to this fact perhaps are traceable the changes which these cell-elements sometimes exhibit during the secretory cycle. But the center for the actual differentiation of visible secretions is the Golgi apparatus. The immediate source of secretory synthesis lies in the area presided over by the Golgi apparatus, and in that sense the Golgi apparatus may be said literally to produce the secretory droplets. Of many workers on the Golgi apparatus in gland-cells only Benoit ('26) (in certain cases), Parat ('28) (in certain respects) and Beams and Wu ('29) find this conclusion untenable, although a few, like Kopsch ('25, '26) and Urasov ('28), find the evidence still inconclusive.

The vacuome theory

In bringing this review to a conclusion, special mention should be made of a very recent view of the Golgi apparatus incorporated in the so-called vacuome theory of Parat, his recent summary (1928) of which gives complete bibliographical references and some rather important modifications of, and additions to the ideas which he expressed in his earlier, brief reports. With this theory we may also connect the views of Corti ('24, etc.) on his so-called 'lacunome.' According to Parat, the classical Golgi apparatus is largely mythical. He holds that the structures so classified really are of several unrelated kinds, such as vacuoles, "active" chondriosomes, diffuse lipoids, etc. Restricting the discussion to gland-cells in vertebrates, however, it is clear that his view of the secretory vacuoles, their morphology and place of appearance, is essentially that already outlined under the Golgi theory. But Parat finds in the Golgi area of other workers, not the classical Golgi apparatus, but a region of "diffuse lipoids" and "active" chondriosomes, in which the primordial secretory vacuoles (vacuome) are distributed. Evidently, the conditions in a gland-cell according to Parat, involve certain ideas which diverge rather sharply from the usual descriptions of the Golgi-area. Nevertheless, Parat's most recent development of the situation *in gland-cells* suggests differences from Nassonov's views which are more in the nature of interpretation than of fact. It would appear from the work of Benoit ('26) and Hirschler and Hirschlerowa ('28) that Parat's "diffuse" lipoidal area is merely another name for what others have called the Golgi apparatus. The primary matter in dispute turns then only on the question of whether this lipoidal material is in a "diffuse" (Parat) or formed (Golgi apparatus) condition (compare also Benoit ('26), Morelle ('27b)). Parat's insistence that the vacuoles (vacuome) are the structures which his predecessors have called the Golgi apparatus seems to me quite without warrant in fact, and is cer-

tainly and conclusively untrue in case of the male germ-cells, where the vacuoles in some cases are the acrosomal material and have never been confused with the Golgi apparatus.

Parat's conception of what he terms the "Golgi zone" in a gland-cell is shown in fig. 19 *B*. It will be observed to differ from fig. 19 *A* chiefly in the importance ascribed to the chondriosomes (his so-called "active" chondriome) in the Golgi area. This conception of "active" condriosomes is entirely new in animal cytology and has been frankly borrowed from Guilliermond's interpretation of the plant chondriome. There is little in the literature at present upon which this conception can find any secure footing, although a certain degree of support is furnished by the observations of Saguchi ('20a), Lewis and Maurer ('20), Urasov ('27, '28), Morelle ('27a), and Tschassownikow ('27). It will be further noted that Parat conceives of the vacuome as the all-important element in the organization of the Golgi zone, while Benoit ('26), Morelle ('27b), and others would view the vacuoles rather as the result of the functioning of the Golgi apparatus. Parat's whole interpretation of the cytoplasm is just now the subject of an acute and universal controversy, and it seems useless to attempt at present any further analysis of his views. But it will be evident that however this controversy may end, the outcome will leave Nassonov's hypothesis in the position of embodying many of the more important morphological features of secretory synthesis.

CONCLUSION

As one regards in retrospect the results of nearly a century of microscopical study of the gland-cell, and more particularly the results of the last fifty years, it is not difficult to see that the cytology of glandular secretion has been almost invariably approached from the wrong starting-point. Instead of beginning with a secretory droplet about to be expelled from the cell, and tracing it back step by step to the material of its origin, we have all too frequently started from some morphological expression of presumed cellular activity and achieved the production of secretory droplets by a single leap—usually speculative. Doubtless this method of approach was largely the result of necessity, since the study of the secretory droplets themselves always ended in frustration exactly at the critical point of their first appearance, due to the inadequacy of technical methods of demonstration.

Now, however, that the various elements of the story have been painfully accumulated, there seems to emerge at last a consistent explanation of the cytological phenomena. Secretion is in essence a phenomenon of 'granule' or droplet formation. Starting with a single such secretory droplet about to be expelled from the cell, we find it possible to trace its origin step by step to a minute vacuole, which has thus from the beginning served as a segregation center for a specific secretion-material. The primordial vacuole is found to arise in that zone of the cell characterized by the presence of the Golgi apparatus, and the evidence indicates, if it does not demonstrate, that the primordial vacuole arises through the activity of the Golgi substance and undergoes a part at least of its development in contact with, or embedded in, the Golgi apparatus. Concerning the place and mode of synthesis of the secretory substances peculiar to a specific kind of secretory-droplet, we have as yet no very tangible understanding. Apparently the Golgi apparatus plays some immediate rôle in the process of accumulation and final synthesis of the secretion-product, but the concomitant

changes in other cellular structures suggest that all parts of the cell contribute in some way. This very probably means that the chondriosomes (and ergastoplasm, if any) are concerned in some indirect manner which is not registered in their morphological history; and further, that the nucleus cooperates in some way with the cytoplasmic area, as registered by its various changes in position, shape, chromaticity, etc. Concerning the exact nature of this nuclear contribution, however, nothing definite can be stated, except that the evidence distinctly indicates that nucleolar extrusions or the other direct nuclear emissions so commonly described in the literature, do not usually play any direct part in the production of a secretory droplet. It may even be doubted whether their occurrence has anything to do with the essential processes of secretory synthesis.

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STUDIES ON THE PHYSIOLOGY OF A GENE

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THE GENES AS AGENTS OF CONTROL IN DEVELOPMENT

IN THE organism the genes play a dual rôle. As essential components of sperm and egg they constitute the known elements of heredity. But they also serve in some measure to control the course of events during development. Genetics treats of them only in the first capacity. In studies on inheritance there is little need, as a general rule, for noting the effects of a gene on the individual except for some single distinctive change. It is only necessary to have a definite external sign indicating the presence of the particular factor in question. Further than this genetics, strictly speaking, is not concerned with the physiological activities of the units with which it deals.

The problems of development have been approached along independent lines. The embryologist has undertaken an analysis of the orderly sequence of events by which the egg becomes a more or less highly differentiated organism from a point of view and by methods which are peculiar to his own field. Current hypotheses offered to account for the phenomena observed have been constructed without reference to the gene. It would appear, however, that there is an increasing measure of interest in the view that no theory of development is of requisite breadth which does not take into consideration the directive influence of the gene complex.

Concerning the nature of gene action, however, our ignorance is almost complete. Knowledge of the genes as hereditary units has passed far beyond an understanding of these entities in their equally important relation to the developmental process.

The student of heredity has long seen in the sharply discontinuous effects of many alternative genetic factors a possible line of attack upon developmental problems. The races he deals with may be looked upon as physiological systems differing in one or more discrete germinal units. He has seen again and again that certain clear-cut changes in the phenotype follow upon the substitution of one allelomorph for another. Might it not be possible, he asks, to trace out the chain of physiological processes linking the superficial effect to the hereditary factor? Such analysis, if successful, should add greatly to an understanding of the character of developmental processes.

In the literature of heredity there is abundant evidence to show that the genes are capable of very precise regulation of developmental phenomena. Factors are known affecting all stages in the ontogenetic cycle and it is a well recognized fact that their action may be large or small. Quite aside from the profound

insight it has afforded into hereditary phenomena is it not, in fact, one of the triumphs of modern biology to have uncovered in the gene complex an orderly, albeit complex mechanism within the cell which guides and controls the manifold processes of the living substance?

In view of the paucity of definite evidence, one can form at present no more than a hazy picture of the real significance of the gene theory for phenomena other than those it was directly invoked to explain. Imagination, therefore, should not be given too free a rein. But to the writer, and I am sure there are other geneticists who hold a similar view, the resolution into its constituent units of one of the two main variables with which the developmental physiologist deals, namely, heredity, can not but mark a very important step forward in opening up new paths by which the problems in this field may be attacked.

In a thoughtful article F. R. Lillie (1927) has recently discussed the mutual relations of genetics and the physiology of development. There is much of interest in the paper that must be passed over here, but I should like to advert briefly to one point of particular importance concerning the possibility of effecting a liaison between these two divisions of biological science. To quote from Lillie's paper, "The progress of genetics and of physiology of development can only result in a sharper definition of the two fields, and any expectation of their reunion (in a Weismannian sense) is in my opinion doomed to disappointment. *Those who desire to make genetics the basis of physiology of development will have to explain how an unchanging complex can direct the course of an ordered developmental stream.*" (Italics mine.) Lillie grants that genes are concerned in the origin of all characters in the organism but regards the widely accepted genetic doctrine that each cell contains the entire complex of genes as a stumbling block to an explanation of differentiation by the action of genetic factors. This, it must be admitted, is a fundamental difficulty. If it cannot be resolved there seems little hope of explaining development on the basis of the genes as primary agents of control and studies of the type to be discussed later in this paper would be futile.

One should not attempt in the present state of our knowledge to formulate a general theory of development based upon gene action which would bridge the gap. There is as yet no adequate basis of fact for such a venture. But it is certainly pertinent to inquire if there is anything illogical or inconsistent in the view that the genes, though the same in every cell, can yet serve as the primary source of control of the highly complex series of changes which these cells undergo in development. I can not find that there is.

It might reasonably be supposed that the genes call forth a consecutive series of reactions, each reaction providing the necessary physiological basis for the succeeding one. Each gene becomes functional when its appropriate substratum emerges in response to the activity of genes already in play. The phenotypic effects show that there is wide diversity in the properties of the individual hereditary elements and it is a logical inference that each gene requires certain specific intra-organic environmental conditions in order to function. If this be granted it follows that the genes will come into action in orderly sequence. While the genes are the same in every cell they will function in an ever-changing way as they alter the circumstances under which they operate. According to this hypothesis each gene comes into play only upon the completion of cer-

tain earlier events primarily controlled by other genes. Each factor may not be physiologically active at all stages. Some genes may be narrowly restricted in their operations; others may function over a wide range of ontogenetic conditions. At one stage in development a particular gene may act in one way and at another stage in a different manner because the milieu has been changed in the interval.

The criticism may be advanced that this view, if sound, merely shifts the problem one stage farther back. But, in a sense, this is all that any scientific explanation can do. We know little concerning the principles governing the unity and integrity of the gene complex in a given species or the specific physiological inter-relationships between the component elements. No answer can be given to the question why certain aggregates of genes form functional sets which come to expression as organisms and others fail to appear as units in the living world. In view of the mathematical possibilities which the genes offer, and granting natural selection, is it not in fact a little surprising that organisms are no more variable than they are? It seems likely that there are laws involved here of first importance for an understanding of developmental processes. Of these we can only express our ignorance and wait for what future investigations may bring forth.

The suggestion that the genes, though remaining the same in every cell, may nevertheless govern differentiation by series of chain reactions, each reaction changing the substratum upon which the gene complex impinges, which, in turn, opens the way for further physiological events, will strike the chemist and the physiologist with a familiar ring. Workers in each of these sciences might furnish numerous examples of systems of this sort in which the essential steps have been determined. It is recognized, of course, that the most complex system with which the physiologist deals is infinitely simpler than the totality of changes involved in development. In the latter we have not only the primary effects of an undetermined number of genes to account for but also a host of side reactions between elements of higher and higher order emerging during the ontogenetic process.

MODE OF ATTACK

Elsewhere the view was expressed (Brink, 1927) that the genes whose primary physiological action should prove most accessible to analysis are those which come into play under conditions in which they do not impinge upon a large number of processes and thus obscure their main properties by secondary effects. Genes conditioning specific reactions late in development should provide, in general, the most suitable material since these encounter the fewest physiological cross-currents. The earlier in ontogeny that a primary differential reaction occurs the greater the likelihood, other things being equal, that some subsequent change will conceal it. Genes directly affecting the character of some end-product in the organism should be particularly suitable for study. Factors controlling the production of certain pigments and especially reserve food materials in plants fall in this category.

THE WAXY GENE IN MAIZE

It was upon the basis of these considerations that the writer in 1925 began a study of the physiological action of the waxy gene in maize (*Zea mays*). Through the changes it occasions in the pollen reserves the waxy gene alters the rate of development of the male gametophyte. This circumstance affords a rather unusual oppor-

tunity for observing the phenotypic effects of the factor. The forepart of the present paper is devoted to a consideration of the results on this phase of the study. In an effort to penetrate further into the physiology of the gene, certain biochemical investigations on the nature of the reserves formed under the action of the waxy factor and the enzyme accompanying them were undertaken. This more difficult aspect of the problem is dealt with in the latter part of the article. The results of the two lines of investigation supplement each other in pointing to the way in which the waxy gene probably functions during development.

The waxy character was first noted by Collins (1909) in some corn received from China. Collins observed that the endosperm of this race differed in texture from that of other varieties of maize. In the mature condition it possesses some of the physical properties of a hard wax and was consequently termed "waxy." In inheritance the waxy character behaves as a simple recessive to the non-waxy condition. Weatherwax (1922) discovered that the endosperm reserves of waxy seeds form a reddish-brown compound when treated with dilute iodine, a characteristic which serves to distinguish this race from all other known forms of maize.

Demerec (1924), Brink and MacGillivray (1924) and Longley (1924) found that the waxy gene affects the character of the pollen also. Whereas the starch granules in the pollen of ordinary races of maize give the typical blue reaction with iodine, the corresponding bodies in pollen from waxy plants assume a reddish-brown color when similarly treated. A parallel difference in the carbohydrate reserves in the embryo sacs was later established (Brink, 1925). In the embryo, leaves, stem, floral organs and other parts of waxy plants the starch grains are identical with those in normal plants in giving a blue color with the iodine reagent. Waxy plants are indistinguishable in appearance from the non-waxy type in the field. The gene, therefore, does not occasion any changes of a general nature in development. Its activity appears to be confined entirely to starch metabolism and is further restricted in that only the reserve starch in pollen, embryo sac and endosperm is affected. The so-called starch of translocation formed in the vegetative parts is the same in waxy and non-waxy plants, at least so far as the iodine test reveals. From the standpoint of accessibility to physiological analysis the localized action of the waxy gene is an important consideration.

Observations on the effect of the waxy gene in the male gametophyte have revealed the significant fact that hybrids between waxy and non-waxy plants produce two kinds of pollen in equal numbers. The one class, staining blue with iodine, corresponds to that formed by the non-waxy parent; the other group, giving a reddish-brown color, is identical with the pollen of waxy plants. In the flowering plants the reduction divisions occur at sporogenesis. It is a logical inference that in the case of these heterozygous waxy plants the one class of pollen grains has received the non-waxy gene and the other equally frequent group, the waxy factor, and that these allelomorphs exert a direct effect in the gametophyte generation.

The gametophyte in the higher plants is a vastly simpler structure than the highly differentiated sporophyte. Manifestation of the action of the waxy factor in the pollen makes possible a study of the physiological properties of this gene without reference to the complications which surround its action in the much specialized diploid plant. And the fact that the gene produces its characteristic effect in the

pollen but two cell generations removed from the reduction divisions indicates that its action may be of a direct sort. That is, the chain of events between end result and the gene may be, comparatively speaking, short and direct.

Effect of the waxy gene on pollen-tube growth

Extensive studies on the inheritance of the waxy character by Collins and Kempton (1911) and by Kempton (1919) show that, on the average, a deficiency of waxy seeds larger than can reasonably be ascribed to chance occurs when heterozygous waxy plants are self-pollinated. On the Mendelian basis 25 per cent of the seeds are expected to be waxy; only about 24 per cent are obtained. This result has been confirmed by a number of investigators. When heterozygous waxy plants are used as staminate parents in combination with the recessive waxy type (*wx wx* ♀ × *Wx wx* ♂) significantly fewer than 50 per cent of the seeds formed are waxy. In the reciprocal cross (*Wx wx* ♀ × *wx wx* ♂) the distribution is in close agreement with Mendelian expectation.

Kempton (1919) suggests that the deficiency of waxy seeds in the above types of matings "could be brought about by a higher death rate for the gametes with the waxy character, or a less vigorous growth of the pollen tubes of such gametes, or a failure of the plants to form the gametes in equal numbers." It has been shown by Brink and MacGillivray (1924) and by Brink (1927) that heterozygous plants produce equal numbers of the two classes of pollen grains within the limits of random sampling, so that the aberrant ratios can not be accounted for on this basis. When it was discovered that *Wx wx* plants produce two equally frequent classes of pollen, the one kind staining bluish with iodine, like that of the non-waxy parent, and the other, reddish-brown as in the waxy variety, Brink and MacGillivray (1924) suggested that the deviation from expectation on Mendelian grounds was probably caused by a differential rate of development of the two classes of male gametophytes. The difference in the character of the reserve materials in the pollen might well provide the chemical basis for such a phenomenon. Thus far attempts actually to follow the progress of pollen tubes in the style of maize have not been successful so that direct proof of this hypothesis is lacking.

If there were a *constant* difference in the rate of growth of waxy and non-waxy pollen tubes in the style we should expect to find a smaller proportion of waxy seeds in the lower half of the ear than in the upper. The farther the pollen tubes travel the greater should be the tendency for the two classes to become separated. Counts on numerous ears show that in general, however, the percentages of waxy seeds on the two halves of the ear are not significantly different. This holds even when the deficiency of waxy seeds is relatively large, as in *Wx wx* plants homozygous for the sugary gene, to be discussed below.

Brink and Burnham (1927), in offering an alternative explanation, point out that two stages in the development of the pollen tube may be recognized. During the first of these the needs of the growing tube are met by the food reserves contributed by the pollen grain, while subsequent elongation is dependent upon supplies from the style. Direct observations on pollen tubes of a number of other species growing on artificial media indicate that the first period is a relatively short one, the pollen reserves being quickly consumed even in the presence of an abundance of nutrients in the culture solution. It is suggested that the waxy gene

exerts a differential effect during the first stage of pollen tube growth only, that is, while the gametophyte is dependent upon its own reserves. During subsequent growth it is assumed that the waxy and non-waxy pollen tubes develop at the same rate.

Support for this view is seen in the fact that the food materials in pollen and style are different. The pollen contains considerable amounts of starch and also fats; the style on the other hand is starch-free, the principal reserves being sugars. Now it has been shown that the waxy gene affects the power of the plant to synthesize starch and it may be inferred that the factor also modifies the reverse process, namely, starch hydrolysis. On this hypothesis there is a chemical basis for differential development of the waxy and non-waxy gametophytes in the early stages of pollen tube growth only.

In the attempts which have been made to explain the deficiency of waxy seeds following combinations in which *Wx wx* plants are used as pollen parents the fact that the ratios on ears from different plants frequently show rather wide fluctuations from the mean value of the population has received particular attention. Kempton (1919) first showed, and his results were confirmed by Brink (1925), that the distributions on ears from matings of this kind do not always form a homogeneous group. The variability in proportion of waxy seeds on individual plants is frequently too high to result from the operation of chance alone. The writer has extensive unpublished data on this situation, which, however, do not point to any satisfactory explanation of the problem. It is reasonably clear that environmental conditions as well as genes other than the waxy-non-waxy pair affect the waxy ratio. No one, however, has yet succeeded in identifying the individual factors at work in either of these complexes. Kempton's (1927) conclusion that storing the pollen from *Wx wx* plants greatly increases the proportion of functioning waxy gametes is not supported by the unpublished results of a recent experiment made by Miss Thelma McWilliams and the writer. In fact our tests showed the opposite effect, namely, that aging the pollen tends to further lower the proportion of effective waxy pollen grains.

In certain of the results obtained by Kempton (1919), Mangelsdorf and Jones (1926) see evidence for the occurrence of an accessory factor linked with the waxy gene which differentially affects the rate of growth of waxy and non-waxy pollen tubes. Indeed these workers assume that the waxy gene itself has a neutral influence and that the disturbances in the waxy ratio are wholly due to an accessory factor. If this explanation is sound the basis upon which the investigations discussed in this paper rest, namely, that there is a causal relationship between the nature of the carbohydrate reserves in waxy pollen and the deficiency in the waxy ratio, is quite false.

One looks in vain, however, for any definite support of their hypothesis in the data Mangelsdorf and Jones use. Kempton's F_2 progenies from selfed *Wx wx* plants gave an average of 23.7 per cent waxy seeds and the F_3 progenies, an average of 24.6 per cent waxy seeds. According to Mangelsdorf and Jones, "The difference between these two generations is 4.3 times the probable error and would be expected as the result of chance only once in about 267 trials." Such a difference, they continue, cannot be explained by the action of the waxy gene itself, but is exactly what would be expected if an accessory factor linked with the waxy gene is involved. Are the authors justified in their conclusion, however, that the

difference in percentage of waxy seeds in the two generations is actually a significant one? It would appear from the result arrived at that the difference has been evaluated in terms of a probable error based upon the familiar Mendelian formula for three to one ratios. But Kempton (1919) himself has shown that the percentage of waxy seeds on the individual ears comprising the two respective populations upon which the net values of 23.7 per cent and 24.6 per cent are based, do not form homogeneous groups. In other words, the values vary around more than one mean. Now the probable error formula mentioned above, which Mangelsdorf and Jones have apparently used, is legitimately applied to massed data only when the conditions determining the appearance of the two classes of segregates are essentially the same in each of the subgroups comprising the population. This requirement is not fulfilled by the material under consideration, as Kempton (1919) has clearly demonstrated. Mangelsdorf and Jones, in ignoring this circumstance, have been misled into attaching a significance to the difference between the F_2 and the F_3 which is not justified by the facts; the probable errors they have used are too low. Moreover, the direct comparison of F_2 and F_3 data obtained from plants grown in two successive years is a doubtful procedure in view of the likelihood that environment conditions affect the waxy ratio to some extent.

Mangelsdorf's (1929) recent use of the same method in evaluating a net difference in the proportion of sugary and non-sugary seeds on ears with long styles and short styles is open to the same criticism. The case is somewhat similar to the waxy one in that the stock appears to involve a gene affecting pollen tube growth. The number of ears which Mangelsdorf obtained is relatively limited. The large variation in the percentage of sugary seeds on the individual ears indicates that Mangelsdorf's conclusion regarding the significance of the difference between the average values for the long-styled and short-styled series may rest upon less secure ground than he assumes.

Mangelsdorf and Jones (1926) find further evidence for their view that the deficiency of waxy seeds is due to an accessory factor linked with the waxy gene in some results which Kempton (1919) has presented on the relative percentages of waxy seeds given by a series of plants on being selfed and intercrossed. It is noted that heterozygous individuals which give less than 25 per cent waxy seeds on selfing tend to show a similar minus deviation when used as pollen parents in intercrosses. Likewise, plants which give a normal ratio on being self-pollinated tend to give a like result when crossed on sib plants. Using a limit set by a minus deviation equal to twice the probable error, Mangelsdorf and Jones place the plants tested in this way in two groups, low and normal, comprising respectively, 10 and 14 individuals. They assume that this distribution arises as a consequence of heterozygosity in one of the parents of Kempton's hybrids for an accessory factor affecting the chances of waxy and non-waxy gametes in accomplishing fertilization. This appears to be an exceedingly slender thread upon which to hang such an hypothesis. If it be admitted that the correlation in the waxy ratios of selfs and intercrosses is entirely due to the inherent character of the pollen parents—and this is open to some question—it does not follow that the results are attributable to the action of an accessory factor linked with the waxy gene. Other explanations not involving linkage as plausible as the one Jones and Mangelsdorf suggest might be set forth. It has been found by Brink

and Burnham (1927), for example, that heterozygous waxy plants homozygous for the sugary gene (*su su Wx wx*) give markedly lower waxy ratios when used as pollen parents than do sibs carrying the non-sugary factor (*Su Su Wx wx* or *Su su Wx wx*). When pollen from the double heterozygote, *Su su Wx wx*, is applied to the double recessive the ratio of waxy seeds in the sugary class is no lower than that in the non-sugary class. In fact the same proportions of waxy seeds are obtained in both classes as in *wx wx* ♀ × *Wx wx* ♂ combinations not involving the sugary gene. This shows that the sugary gene affects the waxy ratio indirectly through some action on the parent sporophyte. Gametes of the types *su Wx* and *su wx* behave differently according to whether the diploid plant from which they are descended is homozygous sugary or carries one dose of the non-sugary gene. This case has been thoroughly studied and shows very clearly that genetic factors may very significantly modify the waxy ratio without acting as differentials in the gametophyte generation. It is quite possible that a part of the variation investigators have found in populations of ears segregating for the waxy character is due to genes acting in the same way as sugary.

The results obtained in the above mentioned studies on the effect of the sugary gene afford additional evidence for the conclusion that it is the waxy factor itself and not a gene linked with it which is primarily responsible for modification of the Mendelian distribution. As has been pointed out elsewhere (Brink, 1927) the deviation in the waxy ratio on single ears in sugary stocks is usually large, obviating much of the difficulty in classifying individuals with respect to departures from the normal value. If the sugary gene were interacting with a gene linked with waxy rather than with the latter factor itself we should expect the waxy ratios in sugary lines to be grouped around three modes, a high, a low and a normal. Tests with 128 different *su su Wx wx* plants in three distinct stocks showed, however, that the waxy ratio was low in 125 cases and not significantly different from normal in the remaining three. When, therefore, the aberrant results obtained in waxy lines are "exaggerated" by introducing the sugary gene in homozygous condition still clearer evidence is obtained that the deficiency of waxy seeds regularly follows the waxy gene.

A condition similar to or identical with, that characteristic of waxy maize has also been described in a few other members of the grass family. Gris (1860) found it in *Oryza sativa* var. *glutinosa*, and Meyer (1886) reports it in *Panicum miliaceum* var. *canditum glutinosum* and *Sorghum vulgare glutinosum*. Longley (1924) notes that it also occurs in *Coix lachryma-jobi*. Parnell (1921) selfed nine F_1 plants following a cross between glutinous and a non-glutinous variety of rice, obtaining 6879 seeds, of which 1587 were of the glutinous type. On the monohybrid basis 1720 individuals of the glutinous sort would be expected, or 133 more than were obtained. Brink and MacGillivray (1924), in calling attention to the statistical significance of this deficiency, suggested that there is a selective action of some sort which discriminates against fertilization by male gametes carrying the glutinous factor. Chao (1928) has made a careful analysis of this case and has shown that, in general, heterozygous glutinous plants produce fewer seeds of the recessive type than are expected on the Mendelian basis. The probable explanation of the deficiency, according to Chao, lies in a lower rate of growth of the pollen tubes carrying the glutinous factor and is to be attributed to

some property inherent in the glutinous gene itself. It is a significant fact that the glutinous character in rice, showing changes in the carbohydrate reserves of endosperm and pollen apparently identical with those in waxy maize, should also involve differential development of the male gametophyte. The parallel behavior of waxy maize and glutinous rice heterozygotes in producing a deficiency of recessives strengthens the view that the genes which are the cause of the change in the nature of the reserves are also directly responsible for modification of the ratio.

In any consideration of the possibility that the irregularities in the waxy ratio may be primarily due to a gene other than waxy the clearly established fact that the latter factor occasions a pronounced differential effect in the male gametophyte which may be demonstrated in the pollen grain by the iodine test should be given due weight. Since the action of the factor is on the food reserves which are directly consumed in the formation of the pollen tube, just the sort of situation is provided which one would expect to lead to a difference in rate of development of waxy and non-waxy gametophytes. This circumstance alone puts the burden of proof squarely upon those who, like Mangelsdorf and Jones, hold a different view.

Summary of the phenotypic effects of the waxy gene

1. The waxy gene is definitely localized in its activity, so far as it has been possible to discern, to the endosperm, the pollen and the embryo sac. It does not occasion any change in the size or form of the plant.

2. In the endosperm, pollen and embryo sac of waxy plants, the carbohydrate laid down differs from that in the same parts of common maize in staining reddish-brown with iodine rather than blue.

3. The starch grains in the other parts of waxy plants such as the embryo, stem and leaves give the typical blue reaction with iodine. So far as can be detected, therefore, the effect of the waxy gene is restricted to the reserve starch only.

4. Heterozygous waxy plants produce two classes of pollen in equal numbers. The starch grains in the one group stain reddish-brown with iodine like those of the waxy race, while the starch grains in the other class give the blue reaction of ordinary starch. This clear-cut effect of the waxy gene in the pollen immediately following the reduction divisions suggests that the gene controls some step in the synthesis of the reserve corbohydrate in a direct and precise way.

5. When plants heterozygous for the waxy gene are self-pollinated or used as staminate parents in crosses with the recessive type a slightly smaller proportion of waxy seeds is formed than is called for on the Mendelian basis. The deficiency is attributed to a lower rate of growth of waxy pollen tubes during the early stages of development when they are dependent upon the reserves stored in the pollen grain.

BIOCHEMICAL STUDIES

The non-waxy and waxy allelomorphs may be looked upon as conditioning a reaction or series of reactions leading, in the one case, to the production of common starch and, in the other, to a carbohydrate of a somewhat different nature, as the iodine test shows. These substances are the final terms in the chain of physiological processes upon which the genes impinge. They are likewise end-products in the general economy of the plant, for they mark the last step in the preparation of pollen and seed for the initiation of new cycles of development. Stored in insoluble form, they remain definitely out of play until conditions favorable for ger-

mination of pollen and seed are met. They are then brought back into the current of metabolic activity by a reversal of the reactions involved in their synthesis. The processes in which this pair of genes is concerned, therefore, are arrested by natural means immediately following the stage at which the factors manifest their differential action. This circumstance is of obvious importance from the standpoint of accessibility to physiological analysis. One is enabled thereby to approach directly the particular change for which the waxy gene is responsible.

In analysing the physiological properties of the waxy gene we have sought first to determine the way in which the peculiar carbohydrate formed in waxy plants differs from common starch. And, secondly, an attempt has been made to find the mechanism responsible for this change.

Preparation of the waxy endosperm reserve carbohydrate in pure form

By adapting the essential steps in the commercial manufacture of maize starch to laboratory conditions, Brink and Abegg (1927) have obtained the reserve carbohydrate occurring in the endosperm of waxy seeds in relatively pure form. The operation is somewhat tedious, but a very effective separation of the extraneous materials can be made and the refined carbohydrate obtained in quantity. The nitrogen content of the purified product was 0.013 per cent on the dry basis. Starch prepared from common maize by the same procedure contained 0.035 per cent nitrogen. These values compare very favorably with the proportion of nitrogen in commercial samples of maize starch.

Form of the granules in waxy pollen and endosperm

The endosperm reserves in the waxy variety are organized in granular form, as in common maize. In both types the particles are of similar size and are disc-shaped with a centric hilum. The waxy granules are slightly more angular in outline than those of the other type. In common maize the starch grains in the pollen are much smaller than those in the endosperm, seldom measuring more than $4\mu \times 1.5\mu$ through their main axes. They are regularly ovoid in shape. In waxy pollen, on the other hand, the granules are frequently dumb-bell shaped but show considerable variation. When examined under polarized light the granules from the endosperm of non-waxy and waxy maize show no clear differences. In both types the figure is usually centric and the lines are commonly at right angles to each other. The bands are possibly more clearly defined in the case of the waxy material.

The two classes of granules react very differently when treated with strong alkali or concentrated chloral hydrate. The form of the waxy sort is much more quickly distorted. The swelling properties in water differ also, but little attention has been given in these studies to the colloidal characteristics of the two carbohydrates.

Color reaction with iodine

Starch from the endosperm of ordinary maize, in common with that from most other sources, forms an intense blue color when treated with the common iodine reagent (1.0 per cent KI, 0.3 per cent I, in aqueous solution). The corresponding substance from the endosperm of waxy seeds when similarly treated gives a compound which is reddish-brown by reflected light. Pastes containing 0.1 per cent of the two reserve materials likewise react very differently to the iodine test. If 5 drops of the iodine solution are added to 10 cc. samples, ordinary starch paste gives

a color by transmitted light described by Ridgway (1912) as Helvetia Blue, whereas the waxy material gives Rood's Violet. The difference is not obliterated by varying the proportions of the reacting substances over a wide range. Similar preparations using the granular reserves of the pollen give the same respective color reactions, namely, Helvetia Blue and Rood's Violet. In its reaction to iodine the waxy reserve substance is quite similar to glycogen.

The color reactions between starch and iodine have been studied from the colloidal standpoint by Harrison (1911). He found that any agency such as alcohol, potassium iodide or heat which tends to increase the degree of dispersion of the iodine particles shifts the color in the direction of blue to red. On this view the ultimate particles of which the waxy reserve is composed would appear to be smaller than those of common starch, thus presenting a greater surface upon which the iodine is distributed. The smaller size in the case of the waxy substance might be the result of a lower degree of "association" of some element common to both the waxy and non-waxy carbohydrates. The term "association" as used in this connection refers to a union between molecules dependent upon some force other than chemical valency.

Proximate analysis of waxy and non-waxy seeds

On the basis of its color reaction with iodine, Weatherwax (1922) concluded that the reserve material in the endosperm of waxy maize is erythrodextrin. This term was first used, it appears, by Brücke (1872), who applied it to the product obtained on roasting starch. Lintner and Düll (1893) contended that roasted starch contained a mixture of dextrins and, by repeated fractional precipitation with alcohol, claim to have prepared a pure erythrodextrin. The substance gave a reddish-brown reaction with iodine, as its name suggests, and, like Brücke's preparation, was readily soluble in water. The reserve carbohydrate in the endosperm of waxy maize gives the reddish-brown color reaction by reflected light but Brink and Abegg (1926) show that it is not soluble in water or in 10 per cent alcohol. The waxy reserve, therefore, does not conform to either of the substances previously described as erythrodextrin.

TABLE 1

Percentage amounts of starch, dextrin and sugar in waxy and non-waxy maize seed based on dry weight

	STARCH	DEXTRIN	TOTAL SUGARS
Non-waxy	57.85	0.90	1.42
Waxy	59.93	1.87	1.70

TABLE 2

Percentage amounts of starch, dextrin and sugar in waxy and non-waxy maize pollen based on dry weight

	STARCH	DEXTRIN	TOTAL SUGARS
Non-waxy	16.28	2.25	10.27
Waxy	14.96	2.24	11.57

Meyer (1886), in describing a similar substance found in the endosperm of *Panicum miliaceum* var. *canditum glutinosum* and *Sorghum vulgare glutinosum*, terms it "red-staining starch." Our own investigations on the reserve material in waxy seeds show that the substance is essentially starch-like in nature and we have applied to it the convenient term, waxy starch.

The results of proximate chemical analyses of waxy and non-waxy seeds are clearly not consistent with the view that the principal reserve material in the waxy endosperm is a dextrin (Brink and Abegg, 1926). In Table 1 the relative amount of starch, dextrin and total sugars in the seed of waxy and non-waxy maize

as determined by the standard method is shown.

The separation of the dextrin fraction from the starch is based upon the solubility of the former in 10 per cent alcohol after removal by appropriate means of the fatty substances and the sugars. It may be seen that the principal carbohydrate of the waxy seed, far from falling in the dextrin group, appears in the starch class. In fact the content of starch in the waxy seed is somewhat higher than that in the non-waxy material. The absolute quantities of dextrin in both kinds of seed are small, amounting to less than two per cent of the dry substance.

Analyses of the pollen from waxy and non-waxy plants reveal a similar situation, as shown in Table 2. The pollen contains a higher proportion of sugars and only about one-quarter the amount of starch found in the endosperm. The important point is, however, that in the two types, waxy and non-waxy, starch and dextrin are present in about the same proportion and that the former is the chief carbohydrate reserve in both.

Composition of the starch grain

Since Nägeli's (1858) pioneer work it has been recognized that the starch grain is not composed of a single homogeneous substance. Meyer (1895) described two constituents which he termed α-amylose and β-amylose, respectively. The former is mainly responsible for the viscosity of starch pastes and is comparatively resistant to diastatic hydrolysis. On the other hand, β-amylose gives a limpid solution in hot water, stains intensely blue with iodine and is quickly converted to maltose by diastase.

Numerous means have been tried to separate the two components. Sherman and Baker (1916) found that when one per cent raw starch was gelatinized in water at 85°C. and centrifuged at the rate of 2400 r.p.m. for 30 minutes in the presence of 0.001 M NaCl it is separated into a lighter, clearer and more limpid layer containing the more soluble constituent, β-amylose, and a heavier, more viscous layer containing the less soluble component, α-amylose.

Common maize starch when treated in this way (Brink and Abegg, 1926) separates into two distinct layers, as Sherman and Baker found in their experiments. The upper layer is comparatively clear and contains only about 8 per cent of the starch present, and the lower is thick and viscous. Waxy starch gives a very different result. It also separates rather distinctly into two portions but the relative volumes occupied by the two layers in the tube and the amounts of starch they contain are quite unlike those in the former case. The upper layer in the centrifuged tube of waxy starch paste is less deep than the corresponding portion of the non-waxy tube but contains about 60 per cent of the total dry matter. The lower layer is much less viscous than the α-amylose fraction of non-waxy starch.

When tested with iodine, both constituents of the waxy starch paste give the color described by Ridgway (1912) as Rood's Violet, whereas the preparations from the non-waxy starch stain the familiar blue. It is clear, therefore, that the difference between the waxy and non-waxy starches is not to be accounted for on the assumption that they are composed of the same two substances but in different proportions.

A biochemical method (Ling and Nanji, 1923) designed to measure the relative proportions of α- and β-amylose in starch has given different results with this material than the procedure of Sherman and Baker. According to Ling and Nanji, the weakly acting amylase of the resting

barley grain, extracted with water and precipitated with alcohol, converts the β-amylose to maltose while the α-amylose portion is scarcely attacked. Duplicate tests on common maize starch, using the precipitated barley diastase method, gave 48 per cent and 47 per cent respectively of the starch hydrolyzed to sugar. A sample of waxy starch paste showed 49 per cent of the starch converted (Brink, 1928). The barley diastase method, therefore, reveals little difference in the content of β-amylose in common and waxy starch. According to this test there appear to be approximately equal amounts of α-amylose and β-amylose in both.

Evidently the centrifugation method of Sherman and Baker and the barley diastase method of Ling and Nanji measure different things. The biochemical test indicates no important difference in the relative amounts of α- and β-amylose; but the substances may occur in quite dissimilar physical conditions in the two starches, accounting for the different results on centrifugation. About 60 per cent of the waxy starch remains in the upper layer of the tube and the lower layer occupies a volume nearly four times that of the corresponding fraction in the non-waxy sample. This indicates that the particles in both fractions of the waxy starch paste are smaller than those in the corresponding portions of the other lot.

Hemicellulose in waxy and non-waxy starch

Schryver and Thomas (1923) have identified a third substance in starch, which they have shown to be a hemicellulose. When a starch paste is treated at 50°C. with malt amylase there appears, in 10 to 30 hours, depending upon the enzyme concentration, a flocculent precipitate. This is the hemicellulose. It gives a blue coloration with iodine but resists digestion on prolonged treatment with amylase. It is not known whether hemicellulose is an integral part of the starch grain or is present as an impurity.

In the present studies it was not possible to make a quantitative estimation of the hemicellulose content of the waxy and non-waxy starches on account of the rather small supply of laboratory-prepared material available. It was evident, however, from the relatively clear appearance of the conversion liquids in a series of tests on rate of hydrolysis of waxy starch with malt amylase that this substance contained practically no hemicellulose. In common maize starch, on the other hand, significant amounts of it are present. Schryver and Thomas (1923) report 3.6 per cent.

The presence of hemicellulose in common maize starch makes it impossible to measure the rate of conversion of the latter substance to maltose under the action of a hydrolytic agent by noting the time required for the solution to lose the power of giving a color reaction with iodine. Owing to the hemicellulose present color is shown by the conversion liquid long after the starch has been digested. In our first experiments (Brink and Abegg, 1926) on the comparative rate of hydrolysis of waxy and non-waxy starch by HCl and by salivary amylase the work of Schryver and Thomas on hemicellulose was overlooked and we were led to erroneous conclusions through the use of a method which is now recognized as inadequate. We found that non-waxy starch paste on treatment with these two hydrolytic agents retained the power to give color with iodine significantly longer than did waxy starch paste and inferred from this result that the latter substance was more easily digested. It appears, however, that the difference may have been due wholly to the fact that the common maize starch contains a considerable amount of

the resistant, blue-staining hemicellulose, whereas the waxy starch is almost free from it.

The sugar formed on treating waxy and common maize starches with amylase

While a number of investigators dissent from the conclusion, the view is widely held that, under the action of amylase, starch is split quantitatively into a single sugar, maltose. Pringsheim (1923) does not consider that satisfactory proof of the formation of but one sugar has been furnished, and Armstrong (1924) believes that the starch molecule contains glucose as well as maltose residues. Ling and Nanji (1923) are more specific. They claim to have shown that, on hydrolysis with malt amylase, β-amylose (amylose) forms maltose, and α-amylose (amylopectin) produces two sugars, maltose and isomaltose. The weight of evidence, nevertheless, seems to be in favor of the conclusion expressed by Maquenne and Roux (1905) that starch is composed entirely of maltose residues.

In determining whether the reserve starches of waxy and non-waxy maize differ with respect to the sugar formed on diastatic hydrolysis the conversions were carried out in two stages. The starch paste was first treated with alcohol-precipitated barley amylase which hydrolyses the β-amylose and leaves the α-amylose practically unchanged. The latter substance was then separated from the other products of the initial conversion and hydrolysed with a very active preparation of malt amylase. The sugars obtained were identified by their reducing power, specific rotation and the osazone test. The detailed procedure is given in a recent paper (Brink, 1928).

β-amylose fractions of the common and waxy starches

After treatment of the starch paste with barley diastase for 24 hours at 50°C. the conversion is stopped by boiling. The liquid is evaporated to a small volume and poured into alcohol, giving a final concentration of 60 per cent. The α-amylose is precipitated and filtered off. The filtrate, containing the conversion products of the β-amylose, is further purified by treatment with 90 per cent alcohol. The concentration or total solids in solution is obtained by the specific gravity method. The reducing power may then be measured iodimetrically and the specific rotatory power determined. In the case of the β-amylose fraction of the common maize starch the constants were as follows: R(reducing power) = 93 and $[\alpha]_D$ (specific rotation) = +144.6°. The corresponding values for maltose are R = 100 and $[\alpha]_D$ = +138°. It seems probable from these results that some material of a dextrinous nature was still present in the solution after the treatment with 90 per cent alcohol. Dextrins would tend to lower the reducing power and increase the specific rotation. On preparing the osazone a clear test for maltose was obtained. A trace of glucosazone was also found but no crystals of the *iso*malt osazone type described by Ling and Nanji (1923) were present. On the basis of these results it is concluded that the sugar formed from the β-amylose portion of non-waxy maize starch is maltose, accompanied by a very small amount of glucose.

The sugars formed on treating waxy starch paste with barley amylase were examined in the same way. The filtrate obtained after precipitating the α-amylose was milky in appearance and proved dif-

ficult to clear. It gave a violet reaction with iodine, showing that some unconverted dextrins were still present in a very fine state of division. The constants determined on the solution were as follows: R = 96.3 and $[\alpha]_D = +132.5°$. A number of osazones were prepared, which showed well-defined crystals of maltosazone and some glucosazone. A few crystals similar to those which Ling and Nanji considered to be *iso*maltosazone were also seen, but these did not occur consistently. The waxy conversion liquid, therefore, contains principally maltose together with small amounts of glucose and dextrins. The latter substances probably account for the fact that the reducing power is below 100 and the rotatory power of the liquid is less than that expected for a solution of pure maltose ($[\alpha]_D = +138°$).

It may be concluded from these findings that the β-amylose portions of the waxy and non-waxy starches are alike in forming maltose on hydrolysis with amylase.

α-amylose fractions of the non-waxy and waxy starches

The α-amylose portion of non-waxy maize starch, precipitated from the barley diastase conversion liquid by 60 per cent alcohol, is obtained as a firm, non-adhesive, non-elastic, white mass sparingly soluble in water. It showed the following constants: R = 13.2 and $[\alpha]_D = +255°$. A sample was treated with an active preparation of malt amylase at 50°C for 96 hours. During this period the hemicellulose separates out as a flocculent precipitate and may be filtered off. The constants on the solution at the end of the conversion period were: R = 104.6 and $[\alpha]_D = +138.1°$. Several osazones were prepared, which on recrystallization were invariably found to contain an insoluble residue, although no precipitate formed during heating. The recrystallized material showed maltosazone and a small amount of glucosazone but no *iso*maltosazone appeared to be present.

The α-amylose fraction obtained from waxy starch is markedly different in its physical properties from the corresponding substance from common maize starch. Whereas the latter is firm, crumbly and difficultly soluble in water, the waxy α-amylose is elastic, sticky and easily dissolved in water at ordinary temperatures. The constants shown were R = 12.6 and $[\alpha]_D = +167°$. While the determination of specific rotation on material of this sort is subject to rather large error on account of the effect of the methods of clearing and filtering, it seems reasonably certain that the optical properties of the waxy and non-waxy α-amyloses are significantly different. What this means, however, is not apparent. The reducing power of the α-amylose is probably due to the liberation of reducing groups in the substance itself by the alkaline iodine solution used in measuring this property. When the fresh α-amylose is treated with active beer yeast no fermentation ensues, showing that neither maltose nor glucose is present.

After 90 hours' conversion with active malt amylase the waxy α-amylose solution gave the constants R = 100.2 and $[\alpha]_D = +133°$. The crystals formed in the osazone test were rather ill-defined in appearance. Some of them simulated those of the *iso*maltosazone of Ling and Nanji (1923). After careful recrystallization, however, a clear test for maltose was obtained with no other type of crystals present. On inoculating a sample of the conversion liquid with beer yeast a vigorous fermentation developed. According to Ling and Nanji (1923) *iso*maltose is not fermentable with yeast, whereas maltose, as is well known, is readily attacked.

These experiments show that the waxy and non-waxy starches are alike in form-

ing maltose on hydrolysis with amylase. The two fractions, α-amylose and β-amylose, examined separately by treating the starch paste first with the amylase of ungerminated barley and subsequently with malt amylase, give the same result. Traces of glucose are found in the conversion liquids and some dextrins are present. The two kinds of starch, however, show no consistent difference in this respect. The experiments afford satisfactory evidence that waxy starch, like common maize starch, is split into maltose, the yield of this sugar closely approaching the theoretical.

This conclusion is of particular interest from the genetic point of view in showing that the starches formed under the action of the waxy and non-waxy genes are alike with respect to the ultimate sugar unit of which they are composed.

Rate of hydrolysis with malt amylase

On diastatic hydrolysis the waxy and common maize starches both produce maltose, showing that they are composed of the same sugar residue. Possibly the essential difference between the two carbohydrates lies in the manner in which the sugar residues are united in the starch molecules. If this is the case one might expect that on treatment with a given amylase preparation the starches would be hydrolyzed at different rates.

In a series of tests (Brink, 1928) designed to measure the comparative rates of maltose formation, highly purified samples of waxy and non-waxy starch prepared in the laboratory were treated with malt amylase under comparable conditions of concentration and temperature. Two preparations of malt amylase were used. The first, employed in only one test, was of comparatively low diastatic power; the other, used in eight experiments, possessed a relatively high activity. The acidity of the starch pastes was adjusted with acetic acid to pH 4.5. In the samples taken for analysis, the amylase was inactivated by boiling and the reducing power determined by the iodimetric method of Baker and Hulton (1920).

In seven of the nine tests maltose was formed more rapidly from the common maize starch than from the waxy starch. In the two remaining trials there was no certain difference in either direction. In one of the tests terminated at 10 hours, where the conditions were favorable for rapid conversion, the difference in rate in favor of the common starch was maintained to the end of the experiment, when the digestion was about 90 per cent complete.

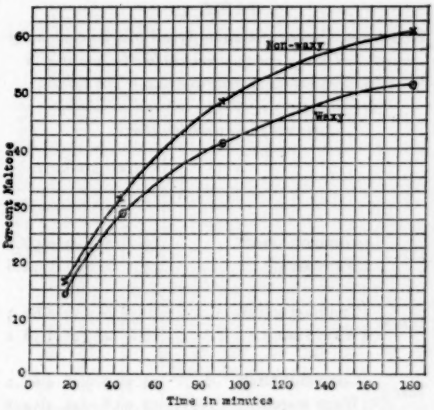

FIG. 1. RATE OF MALTOSE FORMATION FROM THE WAXY AND NON-WAXY STARCHES WHEN TREATED WITH A COMMON ENZYME, MALT AMYLASE. AVERAGE OF RESULTS IN TESTS 7, 8 AND 9

The results of the three tests, numbers 7, 8, and 9, which were carried out with the greatest degree of refinement are given in Table 3 and shown graphically in Figure 1.

The evidence afforded by these experiments clearly favors the conclusion that malt amylase hydrolyses common maize

starch to maltose slightly more rapidly than it does waxy starch. This affords some justification for thinking that there is a structural difference in the molecules of the two carbohydrates.

During the conversion to maltose with malt amylase, waxy starch forms intermediate products of a lower specific rotatory power than does common maize starch. This is shown in Figure 2. If the optically active substances in the conversion liquids are identical in nature, waxy and non-waxy samples containing the same percentages of maltose should have the same specific rotation. It is seen from the figure, however, that the values for common starch stand about 14° higher than those for waxy starch when comparison is made between solutions containing the same amounts of maltose. This means that the intermediate compounds between the initial polysaccharide and the sugar are different in the waxy and non-waxy conversion liquids. If it could be assumed that dissociation of the starch is completed in the initial stages of conversion the difference in optical activity of the solutions might be taken as evidence of a structural dissimilarity in the elementary molecules. It is more likely, however, that dissociation and hydrolysis proceed side by side under the action of the enzyme. If this is the situation, the difference in specific rotation of the respective solutions may be due either to a difference in the simple molecules themselves or to the degree in which the latter are released from some unit of higher order, or to the combined effect of both.

TABLE 3

Comparative amounts of maltose formed from common maize starch and waxy maize starch under the action of a given preparation of malt amylase. The values are percentages of maltose reckoned on initial amount of moisture-free starch

		TIME IN MINUTES			
		15	45	120	180
Test 7	Common starch	13.2	28.4	45.6	59.2
	Waxy starch	13.2	22.8	32.7	42.8
Test 8	Common starch	20.9	36.9	52.8	63.3
	Waxy starch	18.4	34.5	48.3	58.1
Test 9	Common starch	14.9	29.9	46.4	61.2
	Waxy starch	11.9	28.5	42.4	54.2
Average	Common starch	16.3	31.7	48.3	61.2
	Waxy starch	14.5	28.6	41.1	51.7

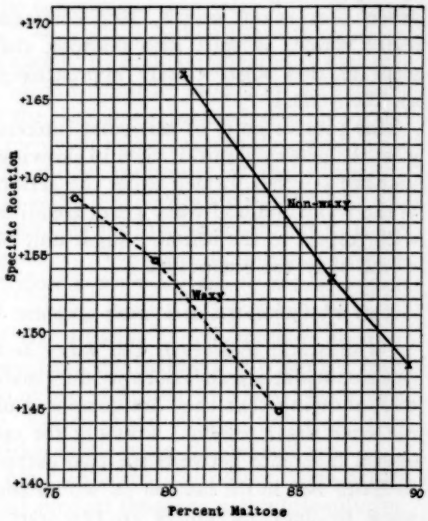

FIG. 2. SPECIFIC ROTATIONS OF THE CONVERSION LIQUIDS DURING HYDROLYSIS OF THE WAXY AND NON-WAXY STARCHES WITH MALT AMYLASE

Phosphorus content of waxy starch

Starch contains a small amount of phosphorus, which is not removed by strong acids and bases. Samec (1914) believes that the substance is present in organic combination. It is an interesting fact, the significance of which, however, is not yet known, that waxy starch contains only about one-twelfth as much phos-

phorus as common maize starch. Duplicate determinations (Brink, 1928) gave 0.0192 and 0.0194 per cent for common maize starch and 0.0016 and 0.0015 per cent for waxy starch. The low content of phosphorus in the waxy starch is not due to a deficiency of this element in the endosperm tissue. Endosperm meal from non-waxy seeds was found to have 0.0519 per cent P whereas comparable waxy endosperm meal contained 0.0507 per cent. While the endosperms of waxy and non-waxy maize contain practically equal amounts of phosphorus, only a minute amount is combined with the former type of starch.

Effect of the waxy gene on amylase production

With evidence at hand for a structural difference in waxy starch the next logical step was a search for the agency by which this change is effected. The first possibility to be explored was that the enzyme concerned in starch synthesis and hydrolysis, namely, amylase, formed under the action of the waxy gene was different from that produced in non-waxy plants. Enzymes have often been suggested as the means by which genes exert their differential influences, but few attempts at experimental verification have been reported. So far as the writer is aware, Onslow (1915) is the only one heretofore who has demonstrated a positive relationship between the production of an enzyme and the presence of a particular gene. He found that chloroform water extracts of the skins of recessive white and yellow rabbits lack tyrosinase, whereas similar preparations from black, chocolate and blue skins contain it.

In the present investigation (Brink, 1929) the enzymatic activity of comparable samples of waxy and non-waxy seeds, seedlings and pollen has been tested. A special effort was made to arrange the conditions of the experiments as simply as possible. To avoid the danger of modifying the activity of the preparations no attempts at purification of the enzymes were undertaken. The dried seedlings, seed and pollen were thoroughly ground, treated with water and the crude extracts tested directly on substrates of three kinds, potato, waxy maize and non-waxy maize starch pastes. The reducing power of the conversion liquids was taken as the measure of hydrolytic activity.

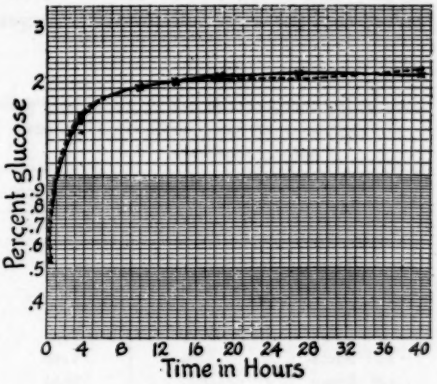

FIG. 3. RATE OF GLUCOSE FORMATION FROM POTATO STARCH PASTE UNDER THE ACTION OF AMYLASE EXTRACTS OF WAXY AND NON-WAXY SEEDLINGS IN TEST 1

Broken line, waxy; solid line, non-waxy

Amylase of waxy and non-waxy seedlings

The waxy and non-waxy seeds on a number of segregating ears were separated and germinated on moist paper. Growth was stopped by drying at 40°C. when the radicles were about one-quarter inch in length. The dried material was finely ground and extracted with water for at least 15 hours. After straining through cheese cloth the diastatic activities of measured amounts of the extracts were tested under appropriate conditions on potato starch paste. Since the material

was not treated with alcohol, maltase was associated with the amylase, producing, as the ultimate product of hydrolysis, glucose rather than maltose. The reducing powers of the conversion liquids were accordingly calculated in terms of the former sugar.

The results of a typical experiment are shown in Table 4 and plotted in Figure 3 using the arith-log scale. On this ruling the same percentage difference is always represented by the same vertical distance so that direct comparison of the rates of hydrolysis may be made. It will be observed that the waxy and non-waxy curves

TABLE 4

Amounts of glucose formed on treating potato starch paste with amylase extracts from ground non-waxy and waxy seedlings respectively. Test 1

TIME	PERCENTAGE GLUCOSE IN SOLUTION	
	Non-waxy extract	Waxy extract
15 minutes	0.53	0.59
48 minutes	0.86	0.90
3.5 hours	1.57	1.58
6 hours	1.72	1.74
10 hours	1.89	1.90
14 hours	2.00	2.00
19 hours	2.07	2.07
27 hours	2.13	2.08
40 hours	2.12	2.18

practically coincide throughout the 40 hour period during which the conversion was followed. This relation was corroborated in a subsequent test. It may be concluded, therefore, that in their diastatic activity the extracts of waxy and non-waxy seedlings are equal.

It is not surprising, in view of the fact that the waxy gene does not exert a differential effect on the starch found in the embryo, that the enzyme extracts of waxy and non-waxy seedlings are equally potent. Both kinds of seedlings are rich in amylase, which appears to be secreted by cells of the embryo adjacent to the endosperm. These same cells, whether *Wx wx* or *wx wx* in composition, during the early development of the seedling lay down an abundance of starch which stains blue with iodine. It appears, therefore, that the waxy gene does not affect the starch formed in this region nor the amylase accompanying it.

THE AMYLASE OF WAXY AND NON-WAXY SEEDS

The dry mature endosperm of the corn seed contains a small amount of amylase. This, presumably, is the residue of the enzyme formed during development of the tissue. It was thought that a study of the diastatic activity of waxy and non-waxy endosperms might throw light on the influence of the waxy gene on the amylase earlier concerned in starch synthesis.

Tests with the mature seed can provide valid evidence on the enzymatic relations prevailing in the two classes of endosperms during the period of starch synthesis only if no differential inactivation of the residual amylase occurs during ripening and storage. Abegg (1929) has obtained evidence which shows that important secondary changes in the fatty substances of the endosperm do occur at these periods. These modifications are of such a nature that it seems very doubtful whether the results of tests on diastatic activity of seeds several months old afford a true picture of the difference which obtains at the time the starch is being laid down. A number of experiments were made with the amylases extracted from mature seeds and a consistently higher hydrolytic activity found in the waxy preparations (Brink, 1928). In view of the above considerations, however, these can not be accorded much significance.

Abegg's investigations show that corresponding changes do not occur in the

pollen grains. On the basis of the facts at hand, therefore, the pollen provides a much more dependable source of material for studying this phase of the problem.

THE AMYLASE OF WAXY AND NON-WAXY POLLEN

Pollen is the material *par excellence* for a study of the action of the waxy gene on amylase production. The pollen grain is a simple, undifferentiated structure which becomes entirely cut off from the parent sporophyte by a heavy wall. The deposition of starch appears to continue until a few days prior to anthesis, so that the enzymes concerned in the process are probably little altered in pollen collected at this time. Maize pollen is readily killed by drying and may be preserved in a thoroughly desiccated condition over calcium chloride for a long period of time without undergoing appreciable change. In pollen taken promptly at the time of shedding and preserved in the non-living condition there would seem to be little opportunity for subsidiary reactions which would significantly alter the character of the amylase formed during starch synthesis.

The absolute amount of amylase in maize pollen is small. In order to obtain a satisfactory measure of its activity it is necessary to prolong the conversions to at least 48 hours and double this time is preferable. In the early stages of hydrolysis the conversion liquid is rather turbid so that small differences can not be accurately established in titration. Later, however, the solutions are clear.

Three tests were made with samples of pollen from closely related waxy and non-waxy plants. The dry pollen was reduced to a fine powder by 36 hours grinding in a ball mill and treated with water over night in the presence of a little toluol to check fermentation. The mixture of powdered pollen and water was then added directly to the starch paste and the amount of glucose formed was measured by the iodimetric method of Baker and Hulton in samples taken at intervals.

In each of the experiments made, the non-waxy pollen showed a higher diastatic power than the waxy. There is a little uncertainty attaching to the differences in rate at the earliest stages, due to the turbidity of the solutions, but as soon as clear readings become possible, larger amounts of glucose are always found in the non-waxy samples.

The results of a typical test (Brink, 1929) carried to 125 hours, with waxy maize starch paste as the substrate, are shown in Table 5 and figure 4. It will be noted that the rate from about five hours onward is clearly higher in the non-waxy than in the waxy lot.

TABLE 5

Amounts of glucose formed from waxy maize starch paste under the action of Su Wx and Su wx pollen extracts. Test 15

TIME IN HOURS	PER CENT GLUCOSE ON STARCH	
	Non-waxy extract	Waxy extract
1	16.57	17.72
9	20.03	19.31
25	24.50	21.32
50	28.82	22.19
75	31.85	23.35
100	35.45	24.64
125	39.20	25.79

As pointed out earlier in the paper, heterozygous waxy plants homozygous for the sugary gene (*su su Wx wx*) give significantly lower waxy ratios when used as pollen parents than do individuals carrying the non-sugary factor. This is attributed to some indirect effect exerted by the sugary gene on the microspores through the parent sporophyte which increases the handicap upon the waxy pollen tubes during the first stage of growth. An

effort was made to determine whether the exaggerating effect of the sugary gene on the waxy:non-waxy ratio is reflected in the diastatic activity of the two sorts of pollen.

The results of three tests on comparable samples of *su Wx* and *su wx* pollen show a consistently higher rate of hydrolysis in the case of the non-waxy pollen but the difference does not appear to be any greater than that for the corresponding classes of non-sugary pollen.

3. On Harrison's view the violet reaction (reddish-brown by reflected light) given by waxy starch paste on treatment with iodine indicates that the particles of which this carbohydrate is composed are smaller than those of common starch. The forces responsible for binding the elementary molecules of starch into units of a higher order, a phenomenon known as association, are not understood. It would appear, however, that the waxy gene exerts an influence on them.

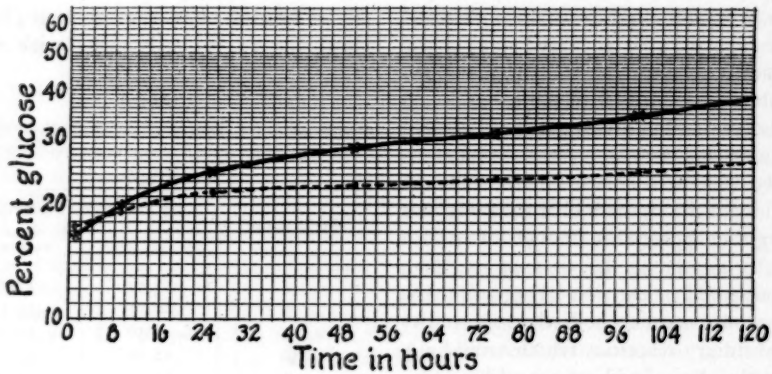

FIG. 4. RATE OF GLUCOSE FORMATION FROM WAXY MAIZE STARCH PASTE UNDER THE ACTION OF AMYLASE EXTRACTS FROM *Su Wx* AND *Su wx* POLLEN

Broken line, waxy; solid line, non-waxy

Summary of the biochemical effects of the waxy gene

1. The carbohydrate stored in the endosperm of waxy seeds when isolated in pure condition is found to be organized in granular form very similar to that of common maize starch.

2. Proximate analyses of non-waxy and waxy seed and pollen show that the principal carbohydrate in both is starch. Very little dextrin is present in either. On the basis of its insolubility in water and in 10 per cent alcohol, the peculiar carbohydrate formed by waxy plants is to be considered a starch rather than a dextrin.

4. When measured by the centrifugation method of Sherman and Baker, waxy starch is found to contain a considerably higher proportion of β-amylose than common starch. The barley diastase method of Ling and Nanji, on the other hand, indicates that the amount of this constituent is nearly the same in the two kinds of starch grains. The discrepancy in the results may be explained on the assumption that the waxy particles are smaller than those of non-waxy starch and consequently behave differently in the centrifuge.

5. Waxy starch contains only a trace of hemicellulose as opposed to 3.6 per cent

reported by Schryver and Thomas for ordinary maize starch.

6. Waxy starch, like the non-waxy sort, forms a single sugar, maltose, on hydrolysis with malt amylase. This shows that the two substances are composed of the same building stones and that the waxy gene exerts its differential effect subsequent to the sugar stage in the formation of starch.

7. Under the action of a given preparation of malt amylase, waxy starch is converted to sugar somewhat more slowly than the non-waxy starch. In explanation of this it is suggested that the maltose residues in waxy starch are linked together in a way slightly different from that in common starch.

8. Waxy starch contains about one-twelfth the amount of organic phosphorus present in the non-waxy sort.

9. Aqueous extracts of waxy and non-waxy seedlings show equal diastatic activity when tested on potato starch paste substrates. Since most of the enzyme contained in the seedlings is produced by cells of the embryo which form blue-staining starch grains in waxy as well as non-waxy seeds, a difference in amylase activity of the seedling extracts is not to be expected.

10. Similar extracts from the two classes of pollen show a consistently higher diastatic activity in the case of the non-waxy type. The difference is displayed on substrates of waxy or non-waxy maize starch and potato starch paste. This fact indicates that the primary effect of the waxy gene may be upon the enzyme amylase.

DISCUSSION

The waxy condition in maize is almost unique among Mendelian characters in the flowering plants in affording an opportunity for studying the physiology of a gene in the haploid generation. In microspore and macrospore, the gene manifests its action immediately following the reduction divisions. The pollen grains and embryo sacs receiving the non-waxy factor lay down common starch as the chief carbohydrate reserve; those to which the waxy gene is transmitted manufacture a different type of starch from the same kind of materials contributed by the parent sporophyte. In what way is the waxy starch unlike the common sort and what is the nature of the change in the mechanism of starch synthesis that leads to the new product?

The problem would be simpler if starch were a substance more amenable to structural analysis. Thus far chemists have been unable to agree on the constitution of this polysaccharide, although it has long been known that it is built up of glucose residues. The number of glucose units in the starch molecule and the way in which they are united, however, are still open questions. Possibly the methods which have proved so effective in revealing the structure of the sugars will be of much more limited value in dealing with this more complex carbohydrate which exhibits colloidal properties. At the present time less direct methods of approach, such as the use of enzymes as exploring agents, hold greater promise of advance.

The present studies make it clear that the difference in the waxy and non-waxy reserve products is primarily in the starches themselves and not in the sugar unit which enters into their formation. Both the waxy and non-waxy starches are split into the same sugar, maltose, on diastatic hydrolysis. The fact that the reaction proceeds at a slightly different rate in the two cases suggests a difference in structure of the starch molecules which puts the one class slightly out of adjustment with the enzyme. As to what the actual change in structure is, the experiments afford no information.

The possibility is not excluded by any of the results obtained that the fundamental molecules of the waxy and non-waxy starches are structurally alike and that the carbohydrates differ in the degree to which their simple units are "associated" or bound together by forces other than chemical valency. In fact the difference in color reaction with iodine and the dissimilar behavior of the starch pastes on centrifugation strongly suggest that the particles of waxy starch are actually smaller than those of the other type. This might be a secondary result, however, of some fundamental difference in the elementary molecules themselves.

The lower diastatic activity of the waxy pollen as compared with that of the non-waxy type is suggestive of the agency by which the waxy gene exerts its effect on the kind of starch formed. The amylases in the two classes of pollen differ either in kind or amount. In view of the catalytic nature of the substances and the fact that the difference in the end-products is a qualitative and not a quantitative one, the former is the more likely. It may be assumed that the immediate effect of the waxy gene is the production of an amylase, slightly different in nature from that formed under the action of the allelomorphic non-waxy factor. The waxy amylase promotes the union of the sugar molecules in starch formation in an abnormal way.

The lower diastatic activity of waxy pollen is in conformity with the facts on pollen-tube growth. In matings of the types *wx wx* ♀ × *Wx wx* ♂ and *Wx wx* selfed, the proportion of waxy seeds is usually slightly in defect of that expected on the Mendelian basis. This deficiency might well follow from a slower development of the waxy pollen tubes due to less rapid hydrolysis of their starch reserves.

A comparison of the mode of action of the waxy and the sugary genes on pollen tubes growth affords some insight into the manner in which the waxy factor probably operates. The sugary gene differentially affects the growth of waxy and non-waxy pollen tubes but only when present in homozygous condition in the parent sporophyte. In other words, *su Wx* and *su wx* male gametophytes arising from *su su Wx wx* plants show a marked difference in ability to effect fertilization whereas the same two classes of pollen from *Su su Wx wx* individuals develop at nearly equal rates. Evidently it is the effect of the sugary factor on the parent diploid plant which counts. The waxy gene, on the other hand, calls forth an immediate response in the pollen as soon as it is segregated from its dominant allelomorph. In contrast to the sugary factor it acts in a direct way. Such a prompt effect is suggestive of an influence on some catalytic agency. The physiological action of the waxy gene seems most intelligible on the assumption that the gene controls the formation of the enzyme amylase which functions directly in starch synthesis.

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THE DETERMINATION OF THE NEURAL PLATE IN URODELES

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PROMORPHOLOGY OF THE URODELE

AN AMPHIBIAN egg when first laid shows but little complexity of structure compared with that of the larva which shortly develops from it. It displays polarity in that one half of the egg is less dense than the other half; and, since the egg soon after laying lies free in its membranes, this lighter half rotates to the top. The upper hemisphere is also darkly pigmented superficially. Internally polarity reveals itself in an increase in the size and concentration of yolk granules from the upper or animal pole to the lower or vegetal pole. The nucleus lies nearer the animal pole.

Careful examination discovers a bilateral as well as a polarized structure in some urodele eggs. The egg of our Pacific newt, *Triturus torosus*, floats with the center of the pigmented area not exactly at the top. A crescent of white is thus to be seen when the egg is viewed directly from above, and in some specimens this crescent is actually of more brilliant lustre than the remainder of the non-pigmented area. Vogt (1926a) describes such a condition in *Amblystoma tigrinum* and in *Pleurodeles*. In other urodeles, the Tritons, for example, such visible evidences of bilaterality are not readily discerned, but experiment has clearly shown that even in such cases the future fates of the two sides are distinguished. Bánki (1928) studied the white crescent of *Amblystoma* and found that it originates in a descent of protoplasm on one side of the egg from beneath the pigment of the animal area. This movement of protoplasm pushes the yolk granules of the vegetal area before it; and the shift in the position of the center of gravity which thus results causes the egg axis to take an oblique direction. Evidence of such a movement of protoplasm in the egg of *Triturus* is occasionally seen in streaks of pigment, torn from the margin of the animal area, which cross the white crescent in a meridional direction. Morgan (1927) accounts for the gray crescent in the frog's egg by a similar movement of substance. Bánki finds some indication of bilaterality in *Amblystoma* even before fertilization has taken place.

Such is the extent of the visible differentiation of the urodele egg when first laid; and throughout the period of segmentation into many cells there is but little increase in observable diversity. The cells of the animal hemisphere are smaller than those of the vegetal hemisphere, and the cleavage cavity which forms within the ball of cells lies nearer the animal pole; but the chemical differentiations which all the while are undoubtedly taking place cannot be visibly demonstrated.

Now, it has been possible by several methods, notably by marking the surface

of the developing eggs with vital dyes, to trace the continuity of materials through the foldings and moldings which follow segmentation, and by reasoning backward to make a map of the surface of the blastula indicating the regions which give origin ultimately to this or to that structure of the embryo. Areas thus distinguished by their future rather than by their present visible diversity have been called *prospective organ rudiments*. Thus we shall refer to the region which becomes the neural plate as *prospective neural plate material*.

Figure 1, taken from Vogt (1926b, 1929) is a schematic charting of the prospective rudiments of the urodele egg at the beginning of gastrulation. The arrow points to the position of commencing invagination. Two transverse lines in the diagram divide the egg into three zones: (1) an upper zone of material (prospective neural plate and epidermis) which increases in area as gastrulation proceeds, until it covers the whole outer surface of the gastrula; (2) a middle zone of cells which descends and rolls beneath the lips of the blastopore, converging toward the dorsal side as it does so, to give rise to the mesoderm and chorda of the primary roof of the archenteron; and (3) a lower zone of material which will be overgrown by the blastoporal margins and become the floor and sides of the enteron—later its definitive roof as well. Roughly, the upper zone corresponds to the pigmented region of the animal hemisphere and the prospective chorda to the crescent, although the relation here is statistical rather than absolute (Bánki, 1927). In *Triturus* there is a small gray area at the vegetal pole which finally comes to occupy a position in the floor of the intestine. Minor subdivisions of the mesoderm are indicated in the figure.

DETERMINATION AS CHEMICAL DIFFERENTIATION

Such diagrams as this one which Vogt has given us bring us face to face with an issue of fundamental importance; namely, to what extent are the different areas of the blastula, prospectively this and that, also potentially the same structures? To what extent are they chemically differentiated, determined as to their fates; or are they indifferent, their determination an event of the future? In a word, are they "pre-primordia"? The experiments thus

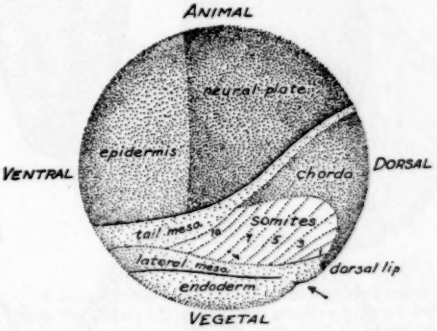

FIG. 1. PROSPECTIVE ORGAN RUDIMENTS OF EARLY GASTRULA

A schematic view of an early gastrula as seen from the left side, indicating the regions which differ according to their prospective fates. The arrow points to the beginning invagination. (Redrawn from Vogt, 1926b.)

far referred to do not answer this question. They serve to trace the continuity of materials during development, but they do not tell us of causal relationships.

In discussing this problem we shall find it of advantage to adopt a positive terminology. There is a negative habit of speech which pictures the progressive specialization of an egg during its development as a "localization," a progressive limitation to definite loci of potentialities already present but more widely distributed. Of this sort are the concepts of

"genetic restriction" and "embryonic segregation" (Lillie, 1929). Now such language has served well, and cannot be gainsaid so long as the potentialities are thought of as purely conceptual things without objective counterpart in nature. To invest them with reality, however, and think of them as corpuscles of some sort, or as chemical stuffs, is to create abstruse problems incapable of solution. Among such are the problems of the origin, nature, and mechanism of localization of the hypothetical entities.

The positive terminology avoids these difficulties. It pictures development (at least so far as the cytoplasm is concerned) as an actual and orderly coming-into-being of diversity, a true epigenesis. First there appears chemical diversity; then, and arising by reason of the chemical diversity, structural differences. The advantage of the positive view is that it does not assume the existence at any moment of development of a greater degree of somatic complexity than can be demonstrated and experimentally investigated.

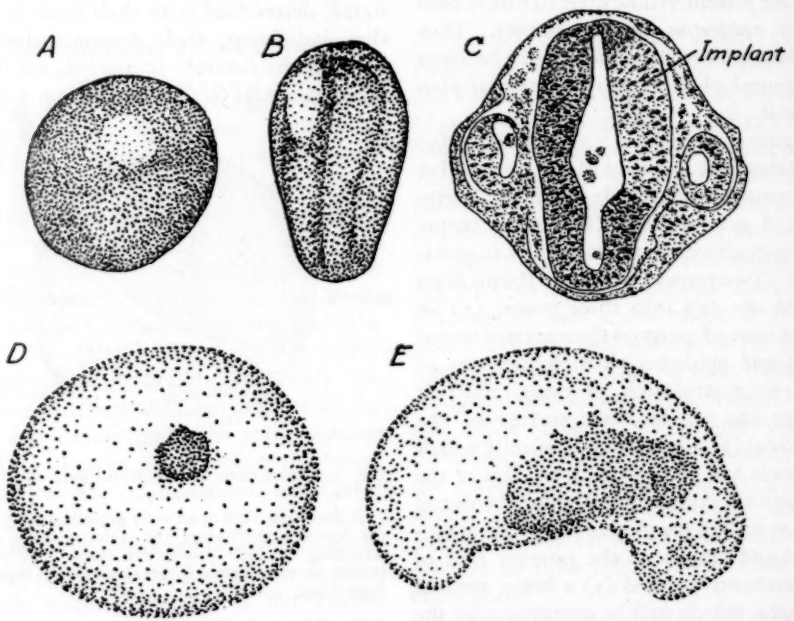

FIG. 2. "RELATIVE INDIFFERENCE" of PROSPECTIVE ORGAN RUDIMENTS

A. A small disc of prospective epidermis from an early *Triton cristatus* gastrula has been implanted in the prospective neural plate area of an early *T. taeniatus* gastrula. *B* and *C*. It has differentiated according to its new location into nervous tissue. *D*. In the converse experiment the disc of prospective neural plate material removed from the *T. taeniatus* gastrula has been implanted in the region of prospective epidermis of the *T. cristatus* gastrula, and (*E*) has differentiated according to its new location as epidermis. (After Spemann, 1921.)

The term now in use to describe specialization positively conceived is the word *determination*. Determination may be defined as that process of invisible presumably chemical differentiation which causally precedes the appearance of a visible organ rudiment. By reason of continued determination the egg, at first indifferent,

becomes more and more a *mosaic*. A region thus actually, although as yet invisibly, set apart may be termed a *pre-primordium* or *chemical rudiment*. The central problem of this review, then, is the determination, that is to say, the chemical differentiation of the pre-primordium of the urodele central nervous sytem.

The best place to begin our discussion of experimental evidence is with the notable work of Spemann and his associates in Germany. Inasmuch as the earlier work (through 1926) has been reviewed in English by de Beer (1927), Morgan (1927), and by Spemann himself (1925, 1927), we shall not find it necessary to consider it in detail. The outstanding method of these investigations, although by no means the only method, has been that of transplanting tissue from one region of one embryo to another region of another embryo, and then noting the effect of the operation on the transplant itself and on the surrounding tissue of the host. The results may be summarized as follows:

(1) During the blastular period, and even at the beginning of gastrulation the different regions of the urodele egg are "relatively indifferent" as to their fates. If small pieces are transplanted they may differentiate according to their new locations (fig. 2). Now, as we shall presently see, this does not prove that they are undifferentiated when transplanted. It shows only that whatever chemical diversity may already be present is labile and capable of being reversed under the influence of new surroundings. (Spemann 1918, 1921; Mangold, 1923; Bytinski-Salz, 1929a.)

(2) An important exception is to be made to this principle, however; Spemann (1918) found that prospective chorda-mesoderm taken from just above the dorsal lip of the blastopore at its first appearance, and transplanted to another region of another gastrula, differentiates, not according to its new location, but according to its original location. Such material, inserted on the lateral or ventral side, produces secondary dorsal structures; namely, secondary neural tube, notochord, and somites. The experimental evidence, therefore, is that the material of the dorsal lip region is already irreversibly determined even in the late blastula; or at any rate it is determined to such an extent that it is not altered under the influence of the new surroundings in which it is placed.

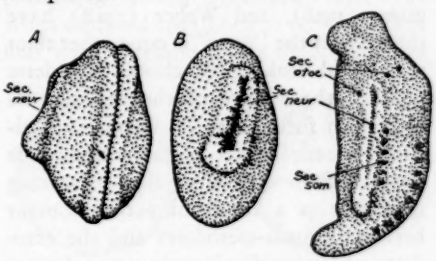

FIG. 3. "ORGANIZER" GRAFT

A disc of prospective chorda-mesoderm (organizer) from the dorsal lip of a *Triton cristatus* gastrula has been implanted on the left side of a *T. taeniatus* gastrula. *A* and *B* are dorsal and lateral views of a later stage of development, and show both the primary and the secondary neural plates. *C* is a still later stage, and shows secondary neural axis, otocysts, and somites, in addition to the structures of the primary axis. (After Spemann and Mangold, 1924.)

(3) Spemann (1918) has carried the analysis further and has shown that the prospective chorda-mesoderm of the dorsal lip acts in development as a "center of organization" in determining the chemical differentiation of the remainder of the egg. It is as though, starting from it, there was a "flow of determination" forward to other regions, notably to the region of prospective neural plate material. It is by reason of this "flow" that the latter becomes a pre-primordium. (See Spemann, 1919; Wessel, 1926.) Furthermore, if dorsal lip material be transplanted

to an indifferent region of another egg, it not only itself differentiates into dorsal structures, but it *induces* the formation of secondary neural plate substance and secondary somites from the substance of the host (fig. 3). On account of this organizing capacity, Spemann has called the material of the dorsal lip, *the organizer*. (Spemann, 1921; Spemann und H. Mangold, 1924; Geinitz, 1925.)

What now is the mode of action of the organizer, and what the nature of the flow of determination? Critical experiments by Marx (1925), Geinitz (1925), Bautzmann (1926), and Weber (1928) have shown that the "flow" is none other than the actual sinking of chorda-mesoderm beneath the surface of the egg and its migration forward to its definitive position beneath neural plate material. It appears from this that the organizing induction is a result of actual contact between chorda-mesoderm and the ectoderm which overlies it; an event analogous to the stimulus by which, at a somewhat later period in development, the contact of the optic cup induces the epidermis to differentiate a lens.

(Suzuki (1928) has shown that the capacity to "organize" nervous tissue is not confined to the chorda-mesoderm of the dorsal side, but is a general property of the entire equatorial belt. Injury to the ventral or lateral prospective mesoderm results in defects in the neural tube in the tail region.)

The picture which this work of Spemann and his students gives is that of a quite undifferentiated egg undergoing determination during gastrulation as a result of the organizing activity of the chorda-mesoderm. But this interpretation has not gone unchallenged. It has been asserted (as by Vogt, Goerttler, and Brachet) that Spemann's results reveal only secondary and "regulative" capacities of the egg, capacities akin to the power of regeneration rather than to the processes of normal development. The criticism brings us face to face with the dilemma of experimental morphology. On the one hand the mere observation of normal development cannot tell us of causal relationships. On the other hand, experimental procedures, if successful, produce abnormal conditions which can be interpreted and applied to normal development only with caution. It is always possible that experimental manipulation may have awakened properties normally in abeyance, and thus have confused the issue. I suppose a large personal element must always enter into one's interpretation of experimental results. I shall return to the significance of Spemann's results presently.

DETERMINATION AS A CONTINUED PROCESS

Recent work, much of which has been reported since the reviews of Morgan and de Beer were written, makes it certain that the differentiation of egg substance begins earlier than the experiments of Spemann and his students might lead one to expect. It has been abundantly shown that the regions of the urodele blastula are not indifferent, but are already differentiated as chemical rudiments.

Vogt (1924) and Mangold (1925) were among the first to make observations which pointed in this direction. They found that pieces of a blastula when transplanted to other regions, although capable of differentiating histologically according to their new locations, nevertheless display a tendency to perform movements typical of their first position. Prospective epidermis, transplanted to a mesodermal region, differentiates into mesodermal structures; but it tends to spread just as it would have spread had it not been transplanted. Prospective meso-

derm, in a similar manner, transplanted to an ectodermal region, carries with it the tendency to invaginate and to stream. Vogt describes the phenomenon very aptly by saying that the regions of the early gastrula are already *dynamically determined* to perform their characteristic movements of gastrulation.

Goerttler (1925) has demonstrated that the material of the blastula previous to gastrulation is also *determined materially*. Instead of transplanting the tissues to new surroundings, as Spemann did, thus bringing them under the influence of changed conditions, he seared the blastoporal lip and thus prevented the normal movements of gastrulation from taking place. He found that prospective neural plate material was able to differentiate *in situ* even when not in contact with underlying chorda-mesoderm (fig. 4). The conclusion is hardly to be avoided that by the end of the blastula stage the material of the neural plate is already determined as to its fate. It is at least a labile pre-primordium.

Recently Vogt (1928b) has discussed the evidence for early determination from another angle. Emphasizing especially the work of Suzuki (1928) he notes that although a defect produced at an early stage in development may heal, and complete restitution of all parts be effected, yet there frequently remains a quantitative weakening in the size and activity of those portions of the embryo which correspond to the region injured. We have here complete qualitative restitution of primordia combined with incomplete quantitative regulation. Thus it is again evident that the blastula is a chemical mosaic.

Vogt (1927, 1928a) finds further evidence of early determination in experiments in which he retarded the development of one half of a blastula while permitting the other half to progress normally. His first method was to embed half of the egg in wax, thus cutting off the oxygen supply to the half. Later he devised a method of fitting the eggs into windows in a thin silver partition, on one side of which there flowed cold water, on the other side water at laboratory temperature. He was notably successful in obtaining the results for which he sought. The favored halves developed apparently normally, while the other halves were retarded. In his 1927 paper he records no effect of the "physiological isolation" of the half on the pattern of its differentiation. The eggs when removed continued to develop, each half with a tempo of its own. The results he terms "age-chimaerae." Later work, however, has caused Vogt to modify his first interpretation; and he now recognizes a decided influence of the environmental factors on differentiation. However, he interprets these effects as secondary and regulative. His general conclusion is that his experiments indicate a considerable amount of chemical differentiation in the cleavage and blastula stages of development which can only be secondarily upset by environmental differences.

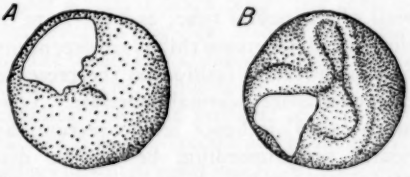

FIG. 4. DIFFERENTIATION OF NEURAL TISSUE INDEPENDENTLY OF MESODERM

A. An early gastrula of Pleurodeles was injured on the left side of the blastopore by means of a hot needle. *B*. The injury prevented the invagination of prospective mesoderm on this side; nevertheless a left neural fold developed. (After Goerttler, 1925.)

Lehmann's work (1926, 1928) bridges the gap between the results which indicate that the determination of the neural plate is early, and those which indicate that it

occurs later, during gastrulation. By a method similar to Goerttler's he injured the dorsal lip of the blastopore with a hot needle at different times during the progress of gastrulation. As a result different regions of the prospective neural plate remained free from underlying chorda-mesoderm. Lehmann finds that under such conditions neural tissue may differentiate even in regions from which chorda-mesoderm is lacking. This is especially true of the region of the neural plate anterior to the otocyst. But, and here is the crucial feature of his work, he finds that the mass and arrangement of nervous tissue, the formation and closure of neural folds, the distribution of nuclei in the wall of the neural tube, and the form of the floor plate—these things are dependent in a quantitative fashion on the presence of a chorda-mesodermal substrate. Lehmann (1928) is hence led to picture the neural pre-primordium before the displacements of gastrulation have occurred as made up of two portions: a central portion (the neural centrum) located toward the anterior end of the neural plate, and a bordering zone which surrounds this and extends backward to the dorsal lip. The centrum is relatively the more completely and irreversibly determined as to its fate. It is least influenced by the lack of mesoderm beneath it. The bordering zone is relatively indifferent, becoming at its margins indistinguishable from the adjacent prospective epidermis. The rôle of the chorda-mesoderm (organizer), in Lehmann's opinion, is to complete and render irreversible the determination of the central portion, and to fix the amount and extent of the bordering zone which shall become nervous tissue. Thus Lehmann's work indicates both the reality of an early determination and the importance of the mesodermal substrate in completing the determination already begun.

Recently Lehmann (1929) by revolving pieces from the margin of the neural plate through 180 degrees, has demonstrated the progressive increase in the determination of the neural plate during the course of gastrulation, as a result of the influence of underlying chorda-mesoderm. And furthermore Mangold (1929), by inserting neural plate material of early, middle, and late gastrulae, and of neurulae into the blastocoele of host gastrulae, has shown a progressive, not a sudden increase in the degree of determination during the course of gastrulation.

There would seem to be four attitudes possible with respect to the evidence now before us. (1) We may with Spemann (see Spemann und Geinitz, 1927) recognize two stages in neural plate differentation, an early and a late. The first takes place early in cleavage, just how early has not as yet been shown. This determination is reversible and incomplete. The second occurs during gastrulation and serves to stabilize and complete what has already been begun. Thus we have here, as elsewhere in development, evidence of a "double assurance" that development shall be orderly and the product of development an adaptive organism. Spemann suggests that both determinations of neural plate material may take place in relation to the chorda-mesoderm; the first as a result of proximity to chorda-mesoderm, the second in consequence of actual contact.

(2) Or we may with Lillie (1929) discount the evidence of an early, labile determination. "There is no doubt that germinal areas possess specific *qualities* at all stages, and that certain of these are essential means of embryonic development;" but this, Lillie believes, does not amount to a determination ("embryonic segregation"). He thinks of determination as a "single decisive event," occupying a very brief interval of time.

(3) Or we may with Vogt, Goerttler, and Brachet stress early determination and interpret Spemann's results as indicative of secondary capacities of the egg, capacities related to regeneration. Not that the early determination is necessarily a complete determination, for it is not; rather it is, to use Vogt's term, a *Bahnung* or preparing of the way for further development. The organization present in the very young egg guarantees the orderly course of later determination. Later development is, as it were, a filling-in of detail.

(4) Neither of these interpretations appeals as quite satisfactory. The concept of "double assurance" conflicts with one's sense of the economy of nature, as does also the assertion that secondary properties exist in the egg. May we not interpret the evidence in terms of a single, long-drawn-out process of determination? The determination of neural plate material begins early in cleavage, if not earlier. It continues with ever increasing definiteness (Lehmann, 1929; Mangold, 1929) as gastrulation progresses, yes, perhaps until the visible rudiment has begun to appear. According to such a concept the early blastula is not indifferent; it is already a chemical mosaic. On this basis it is easy to appreciate that at first determination should be labile and should gradually attain a condition of irreversibility. The early determination, furthermore, is incomplete in that of itself it cannot produce a neural plate of normal mass and structure. We may think of regulation (in developing eggs) as a property related to normal development. It reflects the very mechanism of differentiation. Just as evidence of a mosaic pattern indicates that determination has begun, so the capacity for regulation reveals that determination is still in progress. The importance of the capacity is that it supplies *sustained assurance* throughout the long process of chemical diversification that the final outcome shall be orderly. In the words of Lillie (1927): "The possibility of normal development depends among other things upon flexible but finally precise adjustments of localization (determination) of specific parts everywhere in the embryo."

THE PHYSIOLOGICAL PATTERN OF THE URODELE EGG

The experiments which we have reviewed thus far afford a partial solution of the problem of neural plate determination. They tell us of the time of determination, and something of the conditions under which it takes place; but they do not reveal in any clear fashion the nature of the inducing stimulus. Are we to think of the stimulus as specific, some chemical hormone perhaps; or are we to picture it as non-specific and quantitative, some amount of substance, rate of activity, or oxidative potential, which operates by releasing capacities inherent in the material stimulated? The time is not ripe for an extended discussion of the question. There are lines of evidence, however, mostly of recent date, which indicate that the inducing stimulus is indeed of a non-specific and quantitative nature.

In his Croonian lecture, Spemann (1927) presents evidence that the material of the dorsal lip possesses "longitudinal structure"; also bilateral structure or "laterality." A secondary embryo induced by an implant need not have exactly the same orientation as the primary. In one instance, for example, secondary ear-vesicles formed symmetrically to the right and left of the induced neural plate to which they were related, but they were one behind the other in relation to the axis of the host. Spemann concludes that the

organizer must have "some longitudinal structure, which is not lost by transplantation and which determines the direction of its invagination and consequently of induction." There are limits, however, to the possible lack of harmony between the primary and secondary axes, as Bautzmann (1928a) has clearly shown. Embryonic axes oriented in opposite directions have not been obtained; and

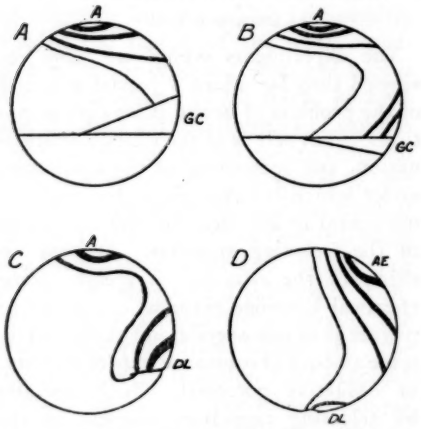

FIG. 5. THE PATTERN OF SUSCEPTIBILITY IN THE DEVELOPING FROG'S EGG

A. In the unsegmented egg disintegration begins at the animal pole but spreads most rapidly toward the grey crescent. *B*. In the many-celled blastula disintegration also begins at the animal pole; but a secondary center soon appears at the future dorsal lip of the blastopore. *C*. Disintegration in the early gastrula begins at the dorsal lip; later at the animal pole. *D*. In the early neurula disintegration begins at the anterior end of the developing neural axis. (*A*, *B*, and *C* are based on figures by Bellamy, 1919. *D* is drawn from descriptions by the same author.)

there is, moreover, a decided tendency for primary and secondary organs of the same nature, for example, otocysts, to differentiate at the same level with respect to the long axis of the egg as a whole. This in itself indicates longitudinal structure. (De Beer, 1927.)

Goerttler (1927) has attempted an experimental analysis of the axiate pattern of the entire egg. Employing a modified form of Spemann's technique he has transplanted quadrangles of tissue from one embryo to another, keeping note always of the orientation of the transplant. He found that pieces of prospective neural plate material of early gastrulae, implanted into the ventral abdominal wall of stages as late as early neurulae, differentiate as small neural plates. But they do this only provided that they were placed in harmonious orientation to the substance of the host; that is, provided they were placed in such position that their dynamic activities in gastrulation and neurulation are unhindered. The experiments clearly indicate the presence of a longitudinal and directional organization.

A further observation of Goerttler's shows bilateral structure in the region of the organizer. Quadrangles from the left side of the blastoporal lip, implanted on the right side of eggs of similar age, invaginated in accord with their dynamic potentialities and contributed to the mesoderm of the host. They also induced secondary neural structures; but, and this is the important feature, the secondary structures were partial, being of left orientation. Thus neurulae were produced possessing two left neural folds but only one right neural fold.

These experiments lead to a concept of the parts of the blastula as possessing an organization which is quantitative and directional. Goerttler pictures the formative forces as strongest and most numerous in the vicinity of the dorsal lip of the blastopore, and as radiating out from there with decreasing vigor to other parts of the egg. The activity and fate of an implant, according to his evidence, depend upon the relation between the dynamic pattern which it brings with it and the pattern of the field into which it is placed.

Such a dynamic pattern, involving as it does longitudinal and bilateral structure,

requires to be visualized in physiological terms. The most available concept to this end would seem to be the hypothesis of physiological gradients as advanced by Child (1921, 1925, 1929). In relation to the present problem the hypothesis involves two main propositions: (1) that the developing egg possesses a physiological pattern or configuration in which different regions differ quantitatively in their relative rates of "metabolic" activity; and (2) that the morphogenic changes which go on in such eggs are related to the physiological pattern. As I see it, the essential feature is not that function precedes structure, but that quantitative differences expressing themselves functionally issue in qualitative differences.

Bellamy (1919) published a paper in which he sought to analyse the functional pattern of the frog's egg at early stages in its development by the method of observing the relative susceptibilities of the different regions to toxic agents. He showed that in this egg, as in organisms generally, the regions of greatest activity are the first to disintegrate when exposed to lethal concentrations of a variety of substances, or to extreme cold. The unsegmented egg begins to disintegrate first at the animal pole, the disintegration spreading most rapidly along the dorsal surface toward the gray crescent or region of the organizer (fig. 5A). In the many-celled blastula disintegration also begins at the animal pole, but there is now a new region of high susceptibility just above the gray crescent in the region which shortly gives rise to the dorsal lip of the blastopore (fig. 5B). With the onset of gastrulation this second region increases in sensitivity; while at the same time the area of susceptibility of the animal pole diminishes (fig. 5C). The condition continues throughout the formation and closure of the blastopore. Just before the neural folds become visible, however, a third region of high susceptibility (Bellamy would identify it with the first) makes its appearance at what will shortly become the anterior end of the neural axis (center of brain area) (Fig. 5D).

These experiments reveal a physiological pattern which is kaleidoscopic, shifting here and there during development as now this region and now that region enters into increased developmental activity. (a) The animal pole is the dominant area before and during the early cleavages of the egg. May we not conceive of it as the high end of the primary gradient in relation to which the materials of the three primary zones of the egg, prospective ectoderm, prospective chorda-mesoderm, and prospective entoderm are first (although as yet reversibly) established? Child (1929) would hold that it also organizes by induction the anterior region of the embryo. The difficulty here is that the animal pole becomes apparently a point of no definite significance in the later development of the embryo (see Kingsbury, 1926). It gives rise to a region of the brain in most urodeles, but to a point in the ventral epidermis in anurans (Brachet, 1927). (b) Physiological dominance now passes to the region of the dorsal lip, which is early established and which soon becomes dynamically the most active region of the egg. It is no doubt in relation to the field of activity of this area that the early, labile chemical differentiation of neural plate material—and no doubt of other materials of the egg as well—is determined. De Beer has expressed this idea in his 1927 review: "There is strong support for the view that the various rudiments become determined at certain levels in a gradient co-ordinate system of which the abscissa culminates at the organizer and the ordinate at the animal pole." I would only change this

by suggesting that a given area is under the influence of the animal pole *before* it comes under the influence of the organizer. How can a region be under the dominance of two centers at one time? The dorsal lip persists for some time as the actively growing tail bud. (c) The third center of metabolic activity at the anterior end of the neural groove is apparently to be correlated with the central area of the neural pre-primordium described by Lehmann (1928). May we not think of it as the dominant region in relation to which the floor, basal, alar, and neural crest areas of the neural plate are established (Kingsbury, 1922)?

EXPERIMENTS WITH THERMAL GRADIENTS

More direct, although as yet not extensive evidence, of the relation between the physiological pattern and the differentiation of the neural plate, is to be found in thermal gradient experiments. Huxley (1927) compressed frog's eggs lightly between two chambers containing water at different degrees of temperature. The eggs were left in their jellies and were surrounded, except where in contact with the walls of the chambers, with humid air. He found, among other results, that warming the upper pole (gradient, "adjuvant") produced a relatively large head; while warming the lower pole (gradient, "antagonistic") produced a relatively large body. Dean, Shaw, and Tazelaar (1928), working in Huxley's laboratory, have continued and extended his studies and have added notes on the effects of transverse temperature gradients; also on the effect of temperature differentials applied to the gastrula and later stages. They record striking asymmetry in the development of the lateral neural folds and mesoderm when one side is warmed. They note further that to a considerable extent, eggs which have been radically upset in the time-relations of their development are able to straighten themselves out and produce forms that are quite normal. Nevertheless, it is certain on the basis of their results, that artificially speeding up the metabolic activity of a part of the neural pre-primordium does actually increase the amount of material which differentiates to form neural tissue. "It would seem that there may exist a 'critical point' as regards the amount of asymmetry capable of regulation."

By a method quite different from that of Huxley, I have (1928) applied temperature differentials to the eggs of the Pacific Coast urodele, *Triturus torosus*. It occurred to me, as it did to Huxley, that if I could modify the physiological pattern by such a gradient, at a definite time and in a definite manner, I should be able to control the invisible differentiation of pre-primordia and affect the formation of visible rudiments. The apparatus employed consisted of a warm and a cold water bath, and of pairs of aluminum plates or "thermodes." The latter conducted the heat between the water baths and opposite surfaces of rows of eggs. Thin agar jelly was used as a medium about the eggs to prevent convection and to support the eggs in place. In one series of experiments eggs in the blastula stage were exposed to a horizontal temperature gradient of five degrees (between egg surfaces) for a period of forty hours. The results seem to have confirmed my thesis. While I was not able to demonstrate to my own satisfaction any effect of a transverse gradient on the fundamental bilaterality of the egg, yet there was produced a pronounced asymmetry. The lateral neural folds which developed on the previously warmed side were commonly larger and more active developmentally than the folds on the cooled side (fig. 6A and B). Moreover, the differences were

clearly not alone those of developmental "age," but involved the differentiation of a larger amount of material into the neural fold of the warmed side. The thermal gradient definitely affected the physiological expression of the blastula at the time when prospective neural plate material was undergoing determination as a pre-primordium.

I would only suggest by way of explanation of this apparently anomalous relation, that if chorda-mesoderm is the dominant region in relation to which neural plate material is established, then the dorso-ventral gradient is "antagonistic" and the ventro-dorsal gradient "adjuvant," and the results are perhaps those which might be expected.

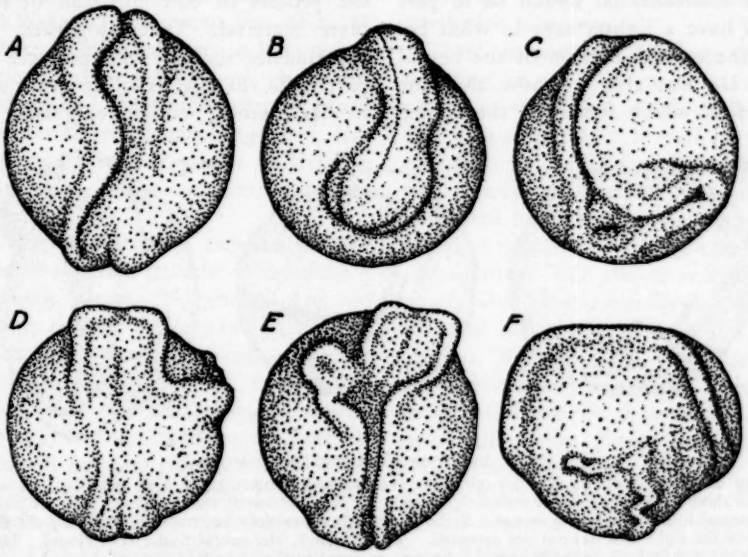

FIG. 6. EFFECT OF THERMAL GRADIENTS ON DEVELOPMENT

Blastulae of *Triturus torosus* were exposed to temperature differentials. *A*. Transverse differentials commonly resulted in a large neural fold on the previously warmed lateral side. *B*. The anterior end of a similar embryo at a later stage in development. Occasionally a secondary neural plate (*C*), an aberrant neural fold (*D*), an accessory brain area (*E*), or puckerings resembling neural folds (*F*) appeared on the previously warmed side. (After Gilchrist, 1928.)

When the gradient was dorso-ventral, the neural plates were sometimes affected in a most unexpected manner. If the dorsal side was warmed they were often smaller, shorter, and with large anterior neural folds. Such results have also been obtained by Dean, Shaw, and Tazelaar (1928); who report also that the converse relationship obtains, there is great proliferation of nervous tissue in specimens cooled dorsally and warmed ventrally.

Reference has been made to the experiments of Vogt (1927, 1928a) in which he subjected eggs to temperature differentials, seeking by cooling to inhibit the development of one half of the egg without at the same time interfering with the normal development of the other half. His aim was "physiological isolation" without morphological isolation. In his 1927 paper he records an effect of his procedure on the rate of development, but no effect

on differentiation, a result rather hard to bring into harmony with the work of Huxley and myself. But in his 1928 papers, Vogt not only shows that the thermal differentials do influence differentiation, but he goes beyond Huxley and myself in demonstrating that they produce an actual shifting of the plane of symmetry of the egg toward the warmed side. The eggs of *Pleurodeles* on which he in part worked have a lighter area in what becomes the central portion of the neural plate. He was able to show that the neural fold which forms on the cooled side arises from near the central portion of this area and is hence whiter than its mate. I observed the same color difference in my work with *Triturus*, but failed to perceive its significance, thinking that the unlike pigmentation was an effect of the thermal gradient, as indeed it may in part have been. Vogt, however, has placed his interpretation beyond reasonable doubt by marking the eggs with vital dyes, and then subjecting them to the thermal treatment (fig. 7). His results show clearly that the neural fold of the cooled side is not only smaller than its mate, but that it arises from a more dorsal position.

Vogt interprets the shifting of the neural axis and the inequality in the sizes of the neural folds as secondary and regulative. In view, however, of the discussion which has preceded, I would hold that they reflect actual processes which at the time are in operation. It remains unquestionably true that the temperature differentials did definitely and profoundly modify the process of determination of neural plate material. Taken together, these experiments indicate the presence of a pattern in the egg, possibly quite simple in its nature, which expresses itself functionally in differentiation, and which can be modified by environmental differentials.

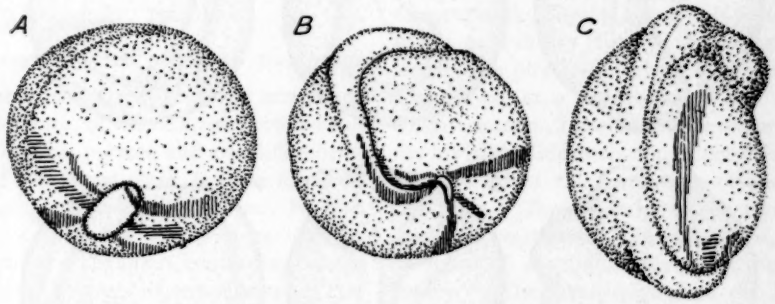

FIG. 7. EFFECT OF A THERMAL DIFFERENTIAL

An egg of Amblystoma at the four-cell stage was marked symmetrically with vital dye. It was then cooled for three days on the future dorsal-right side. *A*. When removed the egg was in the yolk plug stage; the left neural fold has begun to appear. *B*. Later, the left neural fold has risen up, enclosing the three left marks; but the right fold has not yet appeared. *C*. Still later, the neural folds have closed. The three marks on the right which normally would have been enclosed in the right fold remain as epidermis. (After Vogt, 1928a.)

Certain other results of my work with eggs of *Triturus* (1928) bear on this subject. In some eighteen instances secondary neural structures appeared on the previously warmed side of the egg. The implication would seem to be that artificial warming produced secondary regions of high physiological activity in relation to which secondary areas of neural plate material differentiated. It is of interest to note that the later fate of the secondary neural material was influenced by its

relation to other regions of the egg. If it were in the neighborhood of the prospective mesoderm of the blastoporal lips, it became underlain by mesoderm and differentiated as a secondary neural plate (fig. 6C). If it were situated anteriorly, but near the primary neural pre-primordium, it became jointed to the latter and produced an aberrant neural fold (fig. 6D) which sometimes differentiated apparently as an accessory brain area (fig. 6E). If, however, it was forward and ventral in position, removed from both the future mesoderm and the future primary neural plate, it differentiated irregularly into structures resembling neural material in cell structure, but quite different in form (fig. 6F).

Putting the various experiments together we conclude that the differentiation is a long process beginning early in cleavage, or even earlier, and continuing actively throughout the blastula stage and even into gastrulation. It takes place in relation to the physiological pattern of the egg, the dominant center of which is at first the animal pole, but later comes to be the dorsal lip of the blastopore. Thermal gradients impressed upon the egg are able to modify the physiological pattern and by so doing affect the position and form of the neural plate.

THE NATURE OF INDUCTION

So much for the nature of the influences in relation to which the early determination of neural plate material takes place. What of the completion of determination through induction arising in underlying chorda-mesoderm? Is the stimulus in this case also of a quantitative and dynamic nature? Huxley (1924), among others, has suggested that such is indeed the case. "It may well be that it is the stimulus of its (the organizer's) activity as such which causes the neighboring cells to differentiate, as would be expected on Child's theory." Mangold (1928b and c) has gone so far as to suggest that the inducing stimulus is of an electric nature, some definite electric potential, although he apparently favors the view that it is of some simple (i.e., not specific) chemical nature. Child (1929) suggests that induction is of the nature of a transmission of energy rather than a transport of particular substances.

There is perhaps evidence that the inducing stimulus is of a quantitative nature in the recent work of Bytinsky-Salz (1929a and b). It will be recalled that Geinitz (1925) found that prospective chorda-mesoderm of anurans when implanted beneath prospective epidermis of *Triton* is able to induce a neural plate and somites. But the reverse does not occur; the chorda-mesoderm of *Triton* will not induce dorsal structures in the anuran. Bytinsky-Salz has taken implants from gastrulae of both urodeles and anurans and inserted them in the archenterons of young *Triton* gastrulae. He finds that prospective epidermis of the anuran gastrulae is not influenced by its urodele host even though it comes to lie in the very substance of the host's chorda-mesoderm. It develops gland cells and ciliated epidermis just as it would have done had it not been transplanted. Are we to conclude that the inducing capacity of *Triton* is not great enough to affect the rapidly developing anuran tissue? In other experiments of Bytinsky-Saltz prospective neural material of a young gastrula (urodele) was placed in the archenteron of another similar gastrula. In its new location it either fuses with the mesoderm of the primary roof, or with the entoderm of the secondary roof, or with the yolk-laden entoderm of the floor of the archenteron. If it joins the mesoderm it forms (by induction) a neural tube or somites.

If it joins the entoderm of the archenteric roof it may develop in the direction of a neural epithelium. If it joins the entoderm of the floor it gives rise to a tissue without definite structural relationships. Are we to conclude that the capacity of materials to induce varies in quantitative fashion, and that the entoderm is of so low an order of activity that it has no inducing influence on material placed within it?

Somewhat more convincing evidence comes from the discovery of Mangold and Spemann (1927) (working independently) that the optic areas of a neural plate taken from an open neural plate stage and inserted into the cleavage cavity of an early gastrula, will induce the formation of a secondary neural plate. There are two stimuli, therefore, prospective chorda-mesoderm of the dorsal lip and the prospective optic area of the open neural plate, either of which if placed in contact with prospective epidermis of a gastrula will induce a neural plate. Mangold (1928a, 1929) has extended his results. He has found that from the middle yolk-plug stage on to embryos showing muscular activity, portions of the brain have this same capacity, although it is best developed during early neural stages. More surprising still is the fact that limb buds taken from young swimming larvae and placed in a similar position will induce what may perhaps be secondary neural structures. Bautzmann (1928b) has found that a young notochord taken from a neurula will exercise the same function; the mesoderm of the somites, however, retains the capacity to a much less degree. Clearly the induction of a neural plate does not depend upon any specific quality of the implant. In each of the above cases, furthermore, the induced secondary neural plates are of the same age as the primary neural plate, no matter what the age of the implant. The *time* of the determination of neural plate material is correlated with the stage in the development of the host; not with the stage in development of the inducing implant.

The *nature* of the structure which is induced depends upon the host and not upon the implant. It depends first upon the *locus* in the host in which the implant is placed. Bautzmann (1929), for example, has shown that the posterior part of the notochord, implanted in an anterior position, induces the formation of anterior parts. Again, it depends upon the *stage* of the host's development. It has been shown that the same optic rudiment which will induce a neural plate in a gastrula, will, if placed beneath the epidermis of a neurula, induce the formation of a lens. The same stimulus (optic rudiment), acting upon the same material (epidermis of host), but at different stages in its development (gastrula, neurula), produces different results (neural plate, lens). The principle has been well expressed with reference to mammalian development by Lillie (1927): "Thus the embryonic ectoderm of a mammal may be said to have the potencies of nervous system, lens, hairs, glands, and epidermis. But these potencies do not exist simultaneously; when the ectoderm has the potency of forming nervous system, it does not have the potency of forming lens or any primordium of later origin." "The specificity," says Lillie, "lies in the stage and locus, not in the inducing agent."

In view of the above considerations we conclude, at any rate for the present, that the property common to different inducing agents is not specific. It is presumably quantitative in its nature. There is no evidence as yet, however, that qualitative and chemical differences do not enter finally into the inductions by which, as

Lehmann shows, contact with chorda and mesoderm determines the form and structure of the neural plate.

SUMMARY

The principal conclusions derived from the experiments just reviewed may be summarized in the following several propositions:

1. The prospective neural plate material of the urodele blastula occupies a crescent-shaped area situated in the upper hemisphere of the egg just above the prospective chorda-mesoderm of the future dorsal blastoporal lip. The convexity of the crescent extends to the animal pole, its concave margin approximates the equator.

2. Prospective neural plate material attains its definitive position as a neural plate during gastrulation, as a result of movements in which its lower concave margin streams toward the descending dorsal lip of the blastopore.

3. From an early blastular stage the prospective neural plate material is "dynamically determined" to perform these characteristic streaming movements of gastrulation. It is thus already a pre-primordium (chemical rudiment).

4. Prospective neural plate material of the blastula is also partially determined materially in that it is independently able to differentiate histologically into neural tissue. This determination is most advanced in the region (neural centrum) which is to be the central portion of the brain area. The bordering zone is less definitely determined. Like other pre-primordia, neural plate material has at first indefinite boundaries.

5. The determination of neural material which occurs before gastrulation is labile in that it is capable of being reversed under the influence of altered surroundings, as transplantation experiments have shown. The neural plate pre-primordium is as yet "relatively indifferent" as to its fate.

6. The determination of neural plate material is completed during gastrulation as a result of an induction originating in the chorda-mesoderm which comes to underlie it: (a) the determination of the neural centrum is rendered irreversible; (b) the mass and extent of the bordering material which goes to form the neural plate is fixed; and (c) the capacity of the material to form a neural tube of normal structure and arrangement is assured.

7. In all, the determination of neural plate material is a continued process of chemical differentiation, which begins early in cleavage or earlier, continues actively throughout the blastular period, and culminates following the movements of gastrulation. The extensive regulatory properties which exist until the process is well nigh completed are to be thought of as primary capacities of the egg, which reflect the mechanism of determination and supply sustained assurance throughout the long process that the final outcome shall be orderly structure.

8. The determination of neural plate material which occurs before gastrulation, presumably takes place in relation to the longitudinal and bilateral structure which the fertilized egg has been shown to possess. Quantitative differences present in the egg (or in its environment) express themselves functionally as physiological gradients and issue qualitatively in diverse types of chemical activity. Presumably the material of high physiological activity surrounding the animal pole is early differentiated (although reversibly) as prospective ectoderm; then that region of prospective ectoderm which is adjacent to the highly active material of the future dorsal lip becomes determined as neural plate substance.

9. Thermal differentials, impressed upon

the egg at the blastular or early gastrular stages, are capable of modifying the physiological pattern, and thus affect the differentiation of neural plate material.

10. The induction which completes the determination of the neural pre-primordium; namely, that which originates following gastrulation in underlying chorda-mesoderm, may also be quantitative, a response to the high rate of physiological activity of the latter substance. More specific chemical influences may enter, however, in determining the precise form and structure of the neural plate.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

OUR FACE FROM FISH TO MAN. *A Portrait Gallery of Our Ancient Ancestors and Kinsfolk togther with a Concise History of Our Best Features.*
By William K. Gregory.
G. P. Putnam's Sons
$4.50 6 x 9; xi + 295 *New York*

This book will find no favor among the fundamentalists. It is too much to expect them even to glance at the frontispiece where in each of the eleven ancestral types of face they can recognize only too easily characteristic features of many of their friends. Rather will it be a source of pleasure to the semi-scientific readers, who, possessed of a keen sense of humor, enjoy mingling in crowds and studying their fellowmen.

Its chief usefulness will be as collateral reading in the college or university course in evolution. This does not mean that it is burdened with all the characteristics of a text book. One can open its pages almost at random and read with interest the story of how we obtained our face, or, merely by studying the 118 excellent illustrations grasp the salient features of our physiognomistical history. The value of the book to the student is increased by its lengthy list of references and its excellent index.

LIFE PROCESSES AND SIZE OF THE BODY AND ORGANS OF THE GRAY NORWAY RAT DURING TEN GENERATIONS IN CAPTIVITY. *Part I. Life Processes, by Helen Dean King. Part II. Size of the Body and Organs, by Henry H. Donaldson. American Anatomical Memoirs, No. 14.*
Wistar Institute of Anatomy and Biology
$3.50 *Philadelphia*
7 x 10½; 106 (paper)

The original plan of the authors was to determine how far towards the ancestral type (the gray Norway) the albino would revert when placed under wild conditions. The mutant albino differs from the wild type not only in lack of pigmentation, but also in the proportional development of its organs. Five colonies of albinos planted in widely different localities having failed to yield results, the reversed

experiment is now being tried; namely, of rearing the wild ancestral type in captivity.

As the experiment is to continue over a long period of time and will include a very large number of generations, interim reports are to be issued for time to time. This first preliminary report indicates that results of great significance will be reached as the work progresses. It is based on the data collected on 1539 litters containing 4680 males and 4825 females.

The results show that marked changes have occurred in some of the life processes when the tenth generation of Grays is compared with the first. Growth in early life in the tenth generation is much more rapid than in the first generation. Average body weight of adults (both male and female) shows some increase. As the generations advance, the trend of variability in both sexes of captive Grays is towards that found in stock albinos. Average length of reproductive period has increased by about two months due to earlier breeding. There is marked decrease in sterility and mortality in the later generations, also decided changes in behavior.

A number of changes have occurred in the organ constitution of the captive Grays. The tenth generation shows an increase in body weight on body length and a slight increase in the weight of the hypophysis. There is a decrease in weight of the brain, the thyroid, and the suprarenals (especially in the female), the greater loss in all these organs occurring in the first generation. Comparing the tenth generation of the Grays with the albinos, the brain, the suprarenals (especially in the male), the gonads and the bones are still heavy. Body weight on body length and the weight of the thyroid are similar to those for the albino. The hypophysis, especially that of the female, remains less in weight.

REZENTE WIRBELTIERLEICHEN UND IHRE PALÄOBIOLOGISCHE BEDEUTUNG.

By Johannes Weigelt. *Max Weg* 28 marks *Leipzig*

6½ x 10¼; xvi + 227 + 37 plates (paper)

This is an extremely important and interesting book, primarily to paleontologists, but also to naturalists generally. It is a study of how animals die in a state of nature, and what then becomes of their bodies. Weigelt's researches on these problems have been systematic and thorough and throw a flood of light on the interpretation of many puzzling phenomena which have been observed in fossil remains. The book is beautifully illustrated with photogravure plates, most of them based on observations made at various points along the Gulf coast and inland in Texas. We strongly recommend the book to anyone interested in evolution.

TEXTBOOK OF EVOLUTION AND GENETICS.

By Arthur W. Lindsey. *The Macmillan Co.* $3.00 5½ x 8½; xii + 459 *New York*

A well written account of the materials of evolution and genetics and of the theoretical aspects of the subjects. The author aims to hold the balance true between the Darwinian and Lamarckian points of view. The book is a refreshing contrast to most textbooks in its frank recognition of the difficulties still confronting present theories.

THE BOOK OF NATURE. *With the Creator from Season to Season.*
By Marion E. Cady and Frances A. Howell. *Pacific Press Publishing Assoc.*
$1.50 *Mountain View, Calif.*
6 x 7½; xvii + 280

A revised edition of a pious treatise designed to start the young on the right path. It can be recommended to all professors of biology in states having anti-evolution laws. They will find it to be just what they need. For example:

> On the sixth morning of creation week cattle and creeping things and beasts of the earth heard the call of God, and they came forth. What fine-looking cattle browsed in the green pastures! Lions, bears, leopards, cats, tigers, dogs, wolves,—animals of all kinds,—roamed the shady woods, and frisked about with the playful lambs. Creeping things, some very tiny, others larger, crawled through the soft grass from bush to bush and from flower to flower.
>
> What a very happy family they were! Animals of all kinds roamed together, ate together, played together, and lay down to sleep side by side. There was no fear or strife among them. Did the bears growl at the little lambs? Did the wolves pursue the sheep? Oh, no! Even the huge elephants stepped about with care, for they would crush the tiny little creatures beneath their feet.
>
> Such were the beasts God created on the sixth day. Why this peace and friendliness among the animals? Ah, sin was not there! Sin brings hatred and strife. When there is no sin, there is friendliness and love. What a comfortable home these creatures found awaiting them! The cattle found their place in the green pastures, the beasts found their place in the shady woods, and creeping things found downy beds in soft grass. Every creature found his place. It was all so wisely planned by a loving Creator.

We had Reginald the Office Boy read this book, he being the youngest member of the staff, and his only comment was that it should have been printed on thinner paper.

GENETICS

L'INDIVIDUALITÈ DU SANG. *En Biologie, en Clinique, et en Médecine Légale.*
By Leone Lattes. *Masson et Cie*
50 francs *Paris*
6¼ x 9⅛; xi + 314 (paper)

An excellent, thorough discussion of individual differences in human blood, especially with reference to iso-agglutinins and blood grouping. The bibliography covers 55 pages of fine print. The book is clearly written, the material well arranged, and the illustrations well reproduced and to the point in their content. Altogether it is one of the best reference sources on the subject covered that we have seen. Successive chapters deal with the individual reactions of normal blood; the heredity of blood individuality; the individuality of the blood as an anthropological datum; clinical applications of blood individuality; the individuality of the blood in forensic medicine; and technique.

DIE TECHNIK DER BLUTGRUPPEN-UNTERSUCHUNG FÜR KLINIKER UND GERICHTSÄRZTE. *Nebst Berücksichtigung ihrer Anwendung in der Anthropologie und der Vererbungs- und Konstitutionsforschung.*
By Fritz Schiff. *Julius Springer*
8.60 marks *Berlin*
5⅜ x 8¼; vi + 91 (paper)

The second edition of a useful little handbook of bloodgrouping technique. All bibliography is omitted from the edition and the reader is referred to Lattes (*vide supra*) and Hirszfeld particularly for the literature of the subject.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 290.* Containing following articles: *Methoden der Vererbungsforschung bei Tieren*, by Emil Witschi; *Technik der Variations- und Erblichkeitsanalyse bei Crustaceen*, by Richard Woltereck; *Methoden zur Erforschung der Vererbung bei den Lepidopteren*, by Harry Federley.

Urban und Schwarzenberg
10 marks 7 x 10; 190 (paper) *Berlin*

This number of the Abderhalden *Handbuch* will be found useful by all geneticists, particularly the first article by Witschi. It furnishes an excellent introduction to Mendelian analytical technique.

GENERAL BIOLOGY

UNTERSUCHUNGEN ÜBER DIE ENTSTEHUNG AMÖBENÄHNLICHER ZELLEN AUS ABSTERBENDEN INFUSORIEN. *I. Entstehung, Morphologie und Züchtung der Autoplasmen.*
By Hugo Merton. Walter de Gruyter und Co.
2.20 marks *Berlin*
6¼ x 9⅛; 29 (paper)

This is an extraordinary paper, vouched for (at least to the extent of introducing it to the Heidelberg Academy) by Professor Curt Herbst. The author describes the formation of active, living, and reproducing ameboid organisms from the protoplasm of dying infusoria of three genera, *Vorticella*, *Paramecium*, and *Cyclidium*. He calls these new forms *autoplasm*. The observations are detailed, and seem careful and critical. No mention is made of Bastian, who described what seems to be the same thing many years ago under the name of heterogenesis. But then it has long been fashionable among biologists to regard Bastian as a quack and a faker. Evidence, however, seems to be accumulating which indicates that perhaps he wasn't.

CONTRIBUTION À L'ÉTUDE DU PEUPLEMENT DES HAUTES MONTAGNES. *By P. Allorge, R. Benoist, A. Chevalier, L. Chopard, L. Germain, H. Heim de Balsac, R. Heim, H. Humbert, R. Jeannel, L. Joleaud, L. Lavauden, R. Maire, E. de Martonne, C. Motas, P. de Peyerimhoff, E. Pittard, J. Sainte-Clair Deville, R. F. Scharf, B. P. Uvarov and A. Vandel. Paul Lechevalier*
55 francs 6½ x 10; 259 (paper) *Paris*

A collection of some twenty-one essays on various aspects of the ecology of Alpine habitats. Man, mammals, birds, insects, molluscs, water mites, planarians, and plants are the subjects of papers included in the volume. Unfortunately the volume is not indexed, which diminishes its usefulness for reference.

THE PUBLIC AQUARIUM. *Its Construction, Equipment, and Management. Department of Commerce, Bureau of Fisheries Document No. 1045.*
By Charles H. Townsend.
U. S. Government Printing Office
25 cents *Washington*
5¾ x 9⅛; 88 (paper)

This report, by the distinguished Director of the New York Aquarium, will be extremely useful to all those who are in any way interested in the problems of successfully managing aquaria. While it deals especially with the construction, equipment and maintenance of the public aquarium, many of the suggestions will be found invaluable in building and operating laboratory aquaria. The numerous illustrations are well chosen. There are two appendices in which are

discussed the care of the small aquarium and the treatment for removal of chlorine from city water; while in a third section is given, in tabular form, information regarding thirty-two public aquaria throughout the world.

VIE ET REPRODUCTION. *Notions Actuelles sur les Problèmes Généraux de la Biologie Animale.*
By Max Aron. *Masson et Cie*
38 francs *Paris*
$6\frac{1}{8} \times 9\frac{1}{8}$; xi + 366 (paper)

An elementary treatise on general biology, with special emphasis on cytological aspects. The book is intended apparently for popular reading, but will be found interesting by professional biologists and students. It is abundantly and, on the whole, well illustrated.

A LABORATORY STUDY-GUIDE FOR BIOLOGY.
By Charles A. Gramet.
The School Book Co., Inc.
65 cents $8\frac{1}{2} \times 10\frac{3}{4}$; 74 (paper) *New York*

A loose-leaf manual for a high school course in general biology.

THE PROBLEM OF FERMENTATION. *The Facts and Hypotheses.*
By M. Schoen. Translated from the French by H. Lloyd Hind.
Chapman and Hall, Ltd.
21 shillings net *London*
6 x $9\frac{5}{8}$; xii + 211

A remarkably clear presentation of a highly technical subject. The discussions of the hypotheses presented by workers in the various fields of fermentation form by no means the least interesting feature of the book. For the translated edition the author added a new chapter on the rôle of hydrogen in fermentation. A lengthy bibliographical index and subject index add to the usefulness of the book.

HUMAN BIOLOGY

CONSTITUTIONAL INADEQUACIES. *An Introduction to the Study of Abnormal Constitutions.*
By Nicola Pende. Translated by Sante Naccarati. With a Foreword by George Draper.
$3.50 net *Lea and Febiger*
Philadelphia
$5\frac{3}{4}$ x $9\frac{1}{4}$; 270

It is a real service to all students of human constitution to have this book by the leading Italian investigator in the field made available in English. The book is divided into two parts, of which the first deals with the general concepts of constitutional investigation, or as Pende prefers to call it, *biotypology*. The second part is more special, and deals, on the basis of an organological classification, with localized constitutional anomalies and inadequacies. A final chapter is added as an appendix to the English edition giving briefly a systematic outline of the analysis, from the present day point of view, of the individual biotype. The book is an important contribution to the literature of human biology.

BORN THAT WAY.
By Johnson O'Connor.
The Williams & Wilkins Co.
$6.00 $5\frac{1}{4}$ x 8; 323 *Baltimore*

One of the volumes of the "Human

Relations Series." The author sums up the results of several years study on selective tests and the value of the applications of such tests in various industries and occupations. Within limits, the results indicate that it is possible to predict the line of work for which the individual is best fitted, or in which he will best succeed. These tests should be of particular value for those who are at the beginning of a career. "In a single morning one may try a complete set of worksamples, the essences of many occupations, vignettes which introduce the chapters of life, and perhaps prove oneself wholly unfit for half, thereby saving many potential failures and years of wasted striving."

Fully half of the book is taken up with appendices giving an interpretation of "worksample grades" and an extension of the Kent-Rosanoff table.

PRIMITIVE ART.
By Franz Boas.
H. Aschehoug and Co. (W. Nygaard)
$7.75 7 x 9; 376 *Oslo*

In this book Professor Boas gives an analytical description of the fundamental traits of primitive art, illustrated by many examples not only of carving, basketry, weaving, pottery and metal work, but of literature, music and the dance. In all these arts rhythm is an important element. He concludes that geometrical patterns do not grow out of realistic representation.

It is interesting to note that Boas does not agree with Lévy-Bruhl as to the "prelogical" character of primitive thought.

There must have been a time when man's mental equipment was different from what it is now, when it was evolving from a condition similar to that found among the higher apes. That period lies far behind us and no trace of a lower mental organization is found in any of the extant races of man. So far as my personal experience goes and so far as I feel competent to judge ethnographical data on the basis of this experience, the mental processes of man are the same everywhere, regardless of race and culture, and regardless of the apparent absurdity of beliefs and customs.

Some theorists assume a mental equipment of primitive man distinct from that of civilized man. I have never seen a person in primitive life to whom this theory would apply. There are slavish believers in the teachings of the past and there are scoffers and unbelievers; there are clear thinkers and muddle-headed bunglers; there are strong characters and weaklings.

The behavior of everybody, no matter to what culture he may belong, is determined by the traditional material he handles, and man, the world over, handles the material transmitted to him according to the same methods.

Our traditional experience has taught us to consider the course of objective events as the result of definite, objective causation. Inexorable causality governs here and the outer world cannot be influenced by mental conditions. Hence our hesitating wonder at the phenomena of hypnotism and suggestion in which these lines seem no longer sharply drawn. Our cultural environment has impressed this view upon our minds so deeply that we assume as a fundamental fact that material phenomena, particularly outside of the field of human behavior, can never be influenced by mental, subjective processes. Still, every ardent wish implies the possibility of fulfilment and prayers for objective benefits or for help do not differ in principle from the attempts of primitive man to interfere with the uncontrollable course of nature. The credulity with which fantastic theories bearing upon health are accepted, the constant rise of religious sects with abstruse dogmatic tenets, as well as the fashions in scientific and philosophic theory prove the weakness of our claim to a rational view of the world.

Anyone who has lived with primitive tribes, who has shared their joys and sorrows, their privations and their luxuries, who sees in them not solely subjects of study to be examined like a cell under the microscope, but feeling and thinking human beings, will agree that there is no such thing as a "primitive mind," a "magical" or "prelogical" way of thinking, but that each individual in "primitive" society is a man, a woman, a child of the same kind, of the same way of thinking, feeling and acting as man, woman or child in our own society.

DISCOVERIES AND ADVENTURES IN CENTRAL AMERICA.
By Thomas Gann. Charles Scribner's Sons
$5.00 5¾ x 9; 261 *New York*

Mr. Gann continues to discover ruined Maya cities in the jungle and to write in his usual fascinating way about his finds and the wild life which he encounters. We can recommend the book to all those interested in the Maya civilization or in exciting stories of adventure.

THE LAND PIRATES OF INDIA.
By W. J. Hatch. J. B. Lippincott Co.
$5.00 5½ x 8½; 272 *Philadelphia*

An interesting account of the life and habits of the Kuraver, a section of one of the great robber castes of South India. They are trained from babyhood in the arts of deceit and thievery, and become extremely expert at both. In the main they have no fixed abode but live a wandering gypsy life. The book is of real interest to the thoughtful student of human biology, as well as entertaining to the general reader.

THE SAVAGE SOLOMONS AS THEY WERE AND ARE: *A Record of a Head-hunting People Gradually Emerging from a Life of Savage Cruelty and Bloody Customs, with a Description of their Manners and Ways and of the Beauties and Potentialities of the Islands.*
By S. G. C. Knibbs.
Seeley, Service and Co., Ltd.
21 shillings 5¼ x 8½; 282 *London*

A pleasantly discursive account of the author's experiences while acting as a government land surveyor, and later Commissioner of Lands in the British Solomon Islands Protectorate. His observations on anthropological and ethnological matters are too casual to be of much value, but the book makes interesting reading.

URENTWICKLUNG DES MENSCHEN. *Tatsachen und Gedanken.*
By Artur Neuberg. *C. Bertelsmann*
13 marks *Gütersloh*
6½ x 9½; viii + 426

The author of this treatise is an *evangelische Theolog*, of the Lutheran persuasion. It is a *résumé* of all science, but especially biology and geology, from the point of view of an intelligent, widely read parson. As a "reconciler," and that is what it is all about, Pastor Neuberg makes the current American practitioners in this domain seem shoddy. His bibliography and notes run to over 25 pages of fine print. For those who like this sort of thing it is quite the best book of its kind we have seen. It is a pious scientific tract, which does not nauseate.

THE BEAUMONT FOUNDATION LECTURES. *Series Number Seven. I. Human Constitution. Its Significance in Medicine and How it May be Studied. II. The Influence of Sex in Determining Human Disease Potentiality. III. The Patient and His Physician.*
By George Draper.
The Williams & Wilkins Co.
$1.00 5⅛ x 8; ix + 75 *Baltimore*

The three papers which make up this little volume constitute the seventh series of Beaumont Foundation Lectures before the Wayne County Medical Society. The first two essays will serve as a useful and entertaining introduction to the general biological reader who wants to know something of the present viewpoint

regarding the study of constitution in relation to disease. Unfortunately the preparation of the material for printing has been very carelessly done. Errors in spelling authors' names and similar slips mar an otherwise commendable volume.

PHYSICAL EDUCATION IN CITY PUBLIC SCHOOLS. *Physical Education Series No. 10.*
By Marie M. Ready.
U. S. Government Printing Office
15 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{8}$; iv + 100 (paper)

As the result of a questionnaire sent to the superintendants of schools and directors of physical education of a large number of cities, we find in this bulletin much detailed information about physical education practices in American public schools. How far these data will serve the inquirer desirous of assessing the effectiveness of our physical education program is another question. From the table on special costumes required in the gymnasium we learn that in Hannibal, Mo. and other cities "only shoes are required." To a ribald mind the interpretation of this might seem ambiguous.

AN ANALYSIS OF LIFE. *An Attempt to Conduct an Independent Enquiry into the Leading Problems which Confront Mankind. By Harold Clunn. Simpkin, Marshall, Ltd.*
5 shillings net *London*
$5\frac{3}{8}$ x $8\frac{1}{2}$; xxiv + 247

This is a quasi-religious and ethical tract rather than a biological one. Its philosophical position is bred out of Pollyanna by a Monist. The author forecasts

> a glorious future for the human race, when the present day standards of morality and intellect, great as these may now appear to a considerable number of people, will be superseded by the higher standards of conduct which have been built up and improved upon by countless succeeding generations, each of which has profited by the increased experience of its predecessor. When that stage in the history of mankind has been reached, the present-day standards of morality and conduct may even appear almost as primitive as those of the Stone Age seem to the most advanced peoples of our own time.

UNDISCOVERED AUSTRALIA. *Being an Account of an Expedition to Tropical Australia to Collect Specimens of the Rarer Native Fauna for the British Museum, 1923–1925.*
By Sir G. H. Wilkins. G. P. Putnam's Sons
$4.50 6 x $8\frac{3}{4}$; xiii + 353 *New York*

An unimportant but fairly interesting account of the well-known author's travels in Australia while collecting material for the British Museum (Natural History). Speaking of the natives assembled at the Mission Station on Milingimbi, one of the Crocodile Islands, Wilkins makes the following observation (p. 157):

> A curious physiological feature was noticed in many of these unclothed people. They exhibited two or three joints of the lower vertebrae in the form of a tail. The tail was not so noticeable on these people as it is on some of the African tribes, but the tails were quite conspicuous enough to show in a photograph.

Facing page 145 is a photograph of a woman showing one of these "tails." More and more convincing evidence about them would have been welcome. Reginald our Office Boy, who has fundamentalist leanings, but is otherwise sceptical, says that the thing photographed looks to him more like a misplaced wen than a tail.

TRAVELS AND SETTLEMENTS OF EARLY MAN. *A Study of the Origins of Human Progress.*
By T. S. Foster. Frederick A. Stokes Co.
$7.50 6 x 9⅜; 320 *New York*

This is perhaps the best synthesis that has yet been written about our present knowledge of prehistoric man. Certainly we have seen no other attempt at a reconstruction of his life and thought which is based upon so sound and penetrating a philosophic background. The first chapter, which is an essay on history and education in general, is superb. The author's knowledge in the fields of anthropology, archaeology and history is wide and deep. We have noted no errors except trivial and obvious slips of the pen. The work is scholarly without being pedantic. Unfortunately it is not easy reading. The style is heavy and at times involved, and on this account we judge that the publisher's hope for a general audience, which is yearningly expressed in the jacket blurb, will prove a vain one. But to the serious student of human biology we strongly recommend this volume.

CHILDREN IN AGRICULTURE. *U. S. Department of Labor, Children's Bureau Publication No. 187.*
By Nettie P. McGill.
U. S. Government Printing Office
25 cents *Washington*
5¾ x 9; v + 81 (paper)

A summary of the main results of investigations of the work of children in agriculture, obtained from published reports by the Children's Bureau and other sources. Included in the report is a discussion of child labor laws in the various states, a bibliography, and tables (44 in number) exhibiting the number, age, and sex of children engaged in farm work, as well as the type of work performed, prepared from the census data of 1920. It is interesting to note that while there is little legislation anywhere which specifically interferes with the labor of children on farms, except what indirectly comes from compulsory school attendance laws, the only states which in 1920 had more than 10 per cent of the children aged 10 to 15 engaged in agricultural pursuits were Alabama, Arkansas, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, and Texas. As examples of northern farming states for comparison, Illinois had only 0.8 per cent, and Iowa 1.5 per cent.

STUDIES IN PHYSICAL DEVELOPMENT AND POSTURE. *I. The Effect of Exercise on the Physical Condition and Development of Adolescent Boys. II. Bodily Growth with Age. III. Physical Fitness as Reflected in Tests of Muscular Strength. Public Health Bulletin No. 179.*
By Louis Schwartz, Rollo H. Britten and Lewis R. Thompson.
U. S. Government Printing Office
30 cents *Washington*
5¾ x 9; xii + 124 (paper)

These studies are grouped under three headings: The effect of exercise on the physical condition and development of adolescent boys; bodily growth with age; physical fitness as reflected in tests of muscular strength. They comprise part of a plan for an investigation of the effects of occupation in the causation of faulty posture. As no actual data existed which could be used as a basis for the more specialized study, it was necessary to determine statistically the types of posture which might be considered normal for the average individual when occupation was not an important factor. In addition

to numerous measurements of the body there were tests for ascertaining vital capacity, lung force and lung fatigue, and records made of systolic and diastolic blood pressures, and of the pulse at rest, immediately after exercise and two minutes after exercise. Three photographs were taken of each individual. Altogether 2200 individuals living in New York City were examined, all being white males whose parents were born in the United States. Included in the text are 69 tables and 62 figures. This monograph will be a valuable source reference for students of constitution in particular. The results are too detailed and manifold to permit of brief review.

REFRACTIVE ERRORS IN THE EYES OF CHILDREN AS DETERMINED BY RETINOSCOPIC EXAMINATION WITH A CYCLOPLEGIC. *Results of Eye Examinations of 1,860 White School Children in Washington, D. C. Public Health Bulletin No. 182.*
By Grover A. Kempf, Selwyn D. Collins and Bernard L. Jarman.
U. S. Government Printing Office 15 cents *Washington*
$5\frac{3}{4}$ x 9; v + 56 (paper)

An extensive study on the eyes of 1860 white school children of varying ages in Washington, D. C. The work was undertaken to determine "among other things, the real prevalence of refractive errors of various types and degrees at different ages, and whether there is any age period during which myopia or other refractive errors are particularly likely to develop." Homatropin was used as a cycloplegic. The results, too detailed to be given in a brief summary, add valuable data to the literature of anthropometry. In the text are 14 figures and 17 tables, while in the appendix are given further tables of distribution and correlation.

ANTHROPOMETRIE. *Anleitung zu Selbständigen Anthropologischen Erhebungen.*
By Rudolf Martin. *Julius Springer*
4.80 marks *Berlin*
$6\frac{3}{4}$ x $10\frac{1}{8}$; 51 (paper)

This new edition of this well known little handbook of anthropometric technique is practically unchanged from the original edition, beyond the correction of minor errors in proof-reading, etc. Some new illustrations and formulae have been added. It is a standard work in its field.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 289.* Containing following articles: *Die Statistik als Hilfsmittel der klinischen Nosographie,* by Otto Körner; *Methoden zur Bestimmung der Wurzelfestigkeit und des Neigungswinkels menschlicher Haare,* by Adolf Basler; *Über die Methodik der Zellstimulation,* by Methodi Popoff; *Methodik der funktionellen Extremitätentransplantation,* by Paul Weiss; *Bestimmung der Lage der optischen Achse in Biokristallen,* by W. J. Schmidt.
Urban und Schwarzenberg
8 marks 7 x 10; 116 (paper) *Berlin*
Lieferung 292. Die Methoden der konstitutionellen Körperbauforschung.
By Friedrich v. Rohden.
Urban und Schwarzenberg
10 marks 7 x 10; 173 (paper) *Berlin*

The first of the articles in *Lieferung* 289 is an excellent account of the pitfalls which must be avoided in statistical investigations on clinical data. The other articles in this number are perhaps of less importance, and chiefly of general bio-

logical interest. The account of the technique of constitutional studies by von Rohden is excellent, and will be valued by all workers in that field.

CHILDREN OF ILLEGITIMATE BIRTH WHOSE MOTHERS HAVE KEPT THEIR CUSTODY. *U. S. Department of Labor, Children's Bureau Publication No. 190.*
By A. Madorah Donahue.
U. S. Government Printing Office
20 cents *Washington*
$5\frac{3}{4}$ x $9\frac{1}{8}$; v + 105 (paper)

A study for determining the desirability of keeping such children in the custody of their mothers. The cases reported are of 253 children, from 8 years to manhood and womanhood, representing 241 mothers. Twenty-seven organizations in 11 cities made reports on schedule forms prepared by the Children's Bureau. Additional data were obtained in many cases on various phases of the general subject: the personal history and character of the child's father and mother; the effect on the child of the knowledge of his illegitimate birth if he was aware of it, etc.

Social workers have found that mothers who care for their illegitimate children during early infancy will, in most cases, assume responsibility for them permanently, either directly or with the assistance of near relatives. The present study shows that with but few exceptions such children are successfully absorbed into the life of their communities. The best place to bring up an illegitimate child, in short, is in its own family. Thus again has the Children's Bureau achieved a blinding glimpse of the obvious. There is an appendix outlining the method of the investigation.

WANDERINGS IN WILD AUSTRALIA. *In two volumes.*
By Sir Baldwin Spencer. The Macmillan Co.
$17 per set *New York*
$5\frac{3}{4}$ x $8\frac{5}{8}$; xlii + 930

These extraordinarily interesting volumes are packed with information of interest to the anthropologist and the zoologist. The work is composed of the distinguished author's diaries kept during his various expeditions in the Australian bush, edited and expanded. Originally a zoologist, and never losing his interest in that subject, Baldwin Spencer came to be recognized as one of the leading anthropologists and ethnologists of the world.

Because of the wealth of detail recorded in these stately volumes it is impossible to make any brief abstract of the contents. One can only choose special points for mention, which happen to lie in the field of one's own particular interest. For example: We are told that the native recognizes no such thing as natural death. If a person dies he has been killed by someone, either directly or through the intervention of magic. How strong the native's belief on this point is, and also the extraordinary effect which the mind may have on the body, are illustrated by the following quotation (I, pp. 256–257):

> Any native who believes that he has been struck by a charmed spear is almost sure to die, whether the wound be slight or severe, unless he be saved by the counter-magic of a medicine man. There is no doubt whatever that a native will die after the infliction of even a most superficial wound if only he believes the weapon which inflicted the wound had been 'sung' over and thus endowed with *Arungquilta*. He simply lies down, refuses food and pines away. Not long ago a man from Barrow Creek received a slight wound in the groin. Though there was apparently nothing serious the matter with him, still he persisted in saying that the spear had been charmed and that he must die, which accordingly he did in the course of a few days. Another man coming down to

Alice Springs from Tennant Creek contracted a slight cold, but the local men told him that members of a group of about twelve miles away to the east had taken his heart out, and believing this to be so, he simply laid himself down and wasted away. In a similar way a man at Charlotte Waters came to us with a slight wound in his back. He was assured that the wound was not serious, and it was dressed in the usual way, but he persisted in saying that the spear had been 'sung,' and that it could not be seen, yet in reality it had broken his back and he was going to die, which accordingly he did. As the result a party was organised among the members of his group to avenge his death, and the man who was supposed to have wounded him with the charmed weapon was killed.

Instances of occurrences such as these could be multiplied, and though, of course, it is impossible to prove that death would not have followed under any circumstances—that is, whether the native had or had not imagined the weapon to have been 'sung'—yet, with a knowledge of what wounds and injuries he will survive if he does not suspect the intervention of magic, it is not possible to explain death under such circumstances except as associated with the firm belief of the injured man that *Arungquilta* has entered his body, and that therefore he must die.

The volumes are beautifully and lavishly illustrated. They are as fascinating reading as a novel.

SOME PROBLEMS OF LONGEVITY.

By Frederick L. Hoffman. The Spectator Co.

$6.00 5 x 8; x + 180 *New York*

Dr. Hoffman is a vigorous and always interesting writer on public health topics. In the 35 brief chapters in this book he discusses as many different phases of the problem of longevity and related topics, frequently drawing upon his wide knowledge of vital statistics to illustrate his points. Among some of the matters discussed we find: The marital death rate; wasted children's lives; the health of primitive man; the health of the negro; what causes death; social diseases; small pox and vaccination; the human constitution; living underground; tired of life; etc. Unfortunately the book lacks an index.

COMMUNITY HYGIENE.

By Dean F. Smiley and Adrian G. Gould.

The Macmillan Co.

$2.00 5 x 7¾; x + 350 *New York*

In this companion volume to their *College Textbook of Hygiene*, reviewed in our issue of December, 1928, the authors "present those facts concerning the promotion and safe-guarding of public health which they feel should be an essential part of the mental equipment of every college man or woman." The book is interestingly, and on the whole sanely, written, though perhaps a little soft-boiled towards the claims of results from some of the public-health activities.

POSTERITY *in the Light of Science, Philanthropy, and Population.*

By Frank W. White. *Watts and Co.*

2 s. 6 d. net *London*

4¾ x 7⅛; ix + 139

Mr. White is evidently one of the fortunate tribe from whom no secrets are hid. In the 139 pages of his book are given neat eugenic solutions of virtually all the problems with which the British Empire is confronted. We doubt, however, whether the reformer who tried to put the suggested program into practice would find it either as easy or as efficacious as Mr. White himself seems to believe. Major Leonard Darwin, in his Foreword, says that the author is more hopeful than he is.

EXTENSION METHODS AND THEIR RELATIVE EFFECTIVENESS. *U. S. Department of Agriculture Technical Bulletin No. 106.*

By M. C. Wilson.

U. S. Government Printing Office
15 cents *Washington*
5¾ x 9⅛; 47 (paper)

A study of how far the $20,000,000 which is expended annually in the United States for extension work in agriculture and home economics is effective in persuading farmers and their families to adopt the improved practices. In the areas studied the proportion of amenable families ranged from 59 to 96 per cent for agricultural practices and from 10 to 65 per cent for home-economics practices. News stories are the most effective extension method in proportion to their cost.

A STUDY OF ENDEMIC PELLAGRA IN SOME COTTON-MILL VILLAGES OF SOUTH CAROLINA. *Hygienic Laboratory Bulletin No. 153.*

By Joseph Goldberger, G. A. Wheeler, Edgar Sydenstricker and Wilford I. King, with the cooperation of Wm. S. Bean, Jr., R. E. Dyer, J. D. Reichard, P. M. Stewart, M. C. Edmonds, R. E. Tarbett, Dorothy Wiehl, and Jennie C. Goddard.

U. S. Government Printing Office
20 cents. *Washington, D. C.*
5⅞ x 9⅛; vi + 85 (paper)

A careful study of the relation of various demographic, sanitary, economic and dietary factors to pellagra incidence. Among the authors' findings are the following: that endemic pellagra is most frequent in children of from two to fifteen years of age; that the fatality rate is probably not over 3 per cent; that single women, as compared with married, widowed or divorced, are relatively exempt; that 80 to 90 per cent of all cases had their onset from April to July, inclusive; that any association of pellagra with sanitary conditions is a result of the association of both with economic status; that there is a high negative correlation of pellagra with family income; that year-to-year changes in the incidence of the disease parallel changes in economic conditions. The suggested explanation is that these results are caused by differences in the pellagra-preventive value of the diet.

STATISTICAL ABSTRACT FOR THE UNITED KINGDOM *for each of the fifteen years from 1913 to 1927. Seventy-second number.*

Board of Trade (In conjunction with the Ministry of Labour and the Registrar-General).

His Majesty's Stationery Office
6 s. 6 d. 6 x 9⅝; xv + 377 (paper) *London*

The usual well arranged summary containing not only annual figures from 1913 to 1927 but also in many cases decennial figures extending back to 1851 or earlier. We note that while the number of premises licensed to sell intoxicating liquors decreased from 112,371 in 1913 to 101,504 in 1927, a reduction of 9.7 per cent, the number of convictions for drunkenness decreased from 188,877 in 1913 to 65,166 in 1927, a reduction of 65.5 per cent. Apparently prohibition is not the only way of dealing with the alcohol problem.

THE MAKING OF A GREAT RACE. *Racial and Religious Cross-Currents in the United States.*

By Edward A. Steiner. Fleming H. Revell Co.
$1.75 5 x 7⅜; 192 *New York*

In this book, the author, for many years

a student of the immigrant and his problems, presents his views on the cultural value of the three dominant religious groups in the United States—Jews, Roman Catholics, and Protestants—in the making of the future American race. Mr. Steiner is an optimist. His final conclusion is:

> Something, somewhere, assures the bravely humble that here on this continent we may develop a great culture in which the soul of man will be of supreme value; in which personality, not property, will be the measure of achievement, and that a time will come when we will graft all the religious cultures and racial inheritances into unity, making an American culture of universal worth and eternal value.

The book lacks an index.

SPINOZA.
By Leon Roth. *Little, Brown, and Co.*
$3.00 5½ x 8½; xvi + 250 *Boston*

This admirable monograph, by the first professor of philosophy at the Hebrew University of Jerusalem, forms one of the opening volumes of the new "Leaders of Philosophy" Series. It has been written for the general reader as well as the student. The first few chapters are devoted to the life and character of Spinoza, his works and general outlook. The author then enters upon a discussion of the philosophy of the great Dutch scholar, the sources from which he derived his thought and an estimate of his influence upon his contemporaries. Perhaps one of the most valuable contributions which the book makes to the history of philosophy is in the section devoted to the trend of philosophic thought in Spinoza's time. Professor Roth quotes at length from the correspondence between Spinoza and some of his opponents, chiefly Blyenbergh and Tschirnhaus. In these discussions are foreshadowed the reactions of later philosophers to the Spinozian concepts.

THE AMERICAN NEGRO. *The Annals of the American Academy of Political and Social Science, Vol. CXXXX, No. 229.*
American Academy of Political and Social Science
$2.00 (paper) *West Philadelphia*
$2.50 (cloth)
6½ x 9½; viii + 359

A collection of some thirty-nine papers dealing with various aspects of Negro civilization in America at the present time. The material is grouped under seven general heads, as follows: Race relations; the Negro as an element in the population of the United States; the legal status of the Negro; the economic achievement of the Negro; organization for social betterment; race relations in other lands. The volume is edited by Prof. Donald Young. It is an important contribution to human biology.

SOCIETY AND ITS PROBLEMS. *An Introduction to the Principles of Sociology.*
By Grove S. Dow. *Thomas Y. Crowell Co.*
$3.00 5¼ x 7⅞; xiii + 707 *New York*

A revised third edition and fifteenth printing of a book which is widely used as a text-book, as well as by workers in social and philanthropic fields. The edition has been entirely reset and expanded, statistical and other data have been brought up to date and two entirely new chapters on Cultural Forces and Social Processes added. Perhaps the outstanding feature in this edition, when compared with previous ones, is the addition and expansion of much theoretical material, not only in those portions devoted to pure theory, but in other sections of the book as well.

ZOOLOGY

PAPERS FROM THE TORTUGAS LABORATORY OF CARNEGIE INSTITUTION OF WASHINGTON. *Volume XXVI. Publication No. 391.*

Carnegie Institution of Washington
$2.50 (paper) $6\frac{3}{4}$ x 10; 257 *Washington*
$3.50 (cloth)

Among the most interesting of these papers are that of Tennant, Taylor and Whitaker, who find that both halves of a sea-urchin egg, no matter what the plane of section, may form normal identical larvae; Gudger's paper on the teleost fishes of the Tortugas, in which he concludes that it is dangerous to base the classification of tropical fishes on coloration or on the description of a single specimen; Pearse's paper on migration from marine to terrestrial habitats; and Lipman's studies on marine bacteria, which do not bear out the Drew hypothesis of $CaCO_3$ precipitation in the sea through the agency of bacteria.

THE BUREAU OF BIOLOGICAL SURVEY. *Its History, Activities and Organization. Institute for Government Research. Service Monographs of the United States Government No. 54.*

By Jenks Cameron. The Johns Hopkins Press
$2.00 $5\frac{1}{2}$ x $8\frac{5}{8}$; x + 339 *Baltimore*

This is one of the series of monographs in which the Institute for Government Research is dealing with each of the fifty or more distinct services of the government. It describes the background and history of the Biological Survey, its activities of wild life investigation, encouragement, discouragement and protection, and its organization, with the following appendices: Outline of organization; Classification of activities; Publications; Laws; Financial statements; Miscellaneous statistics; and Bibliography. The monograph is well written and will be a valuable source of information.

THE TERRESTRIAL SHELL-BEARING MOLLUSCA OF ALABAMA. *University of Michigan, Museum of Zoology, Miscellaneous Publication No. 18.*

By Bryant Walker. Published in Co-operation with the Geological Survey of Alabama and the Alabama Museum of Natural History.

University of Michigan
$1.00 *Ann Arbor*
$6\frac{3}{4}$ x 10; 180 (paper)

A useful handbook, well illustrated, for the identification of land snails. Workers in other states than Alabama will find it valuable.

THE HERPETOLOGY OF MICHIGAN. *Michigan Handbook Series, No. 3.*

By Alexander G. Ruthven, Crystal Thompson and Helen T. Gaige. Uinversity of Michigan
$1.50 *Ann Arbor*
$5\frac{1}{8}$ x $7\frac{1}{2}$; ix + 229 (paper)

THE WHIP SNAKES AND RACERS. *Genera Masticophis and Coluber.*

By Arthur I. Ortenburger.
University of Michigan, General Library
$6.00 *Ann Arbor*
8 x $10\frac{1}{2}$; xviii + 247

Under the distinguished leadership of its Director, Dr. Alexander G. Ruthven, the University of Michigan has become famous as a center of herpetological research. These two volumes are substantial contributions to the enhancement of this high reputation. The first is a well illustrated handbook for the identification of the amphibia, snakes, and turtles of Michigan. Data on distribution within

the state are given in sufficient detail, in many cases by spot maps. This book will be invaluable to teachers of natural history, nature study, etc.

The second volume noted is a thorough, solid piece of taxonomic research, monographic in character. It is beautifully illustrated by photographic plates as well as line drawings.

CENTENARY HISTORY OF THE ZOOLOGICAL SOCIETY OF LONDON.
By P. Chalmers Mitchell.
Zoological Society of London
25 shillings *London*
5½ x 8½; xi + 307

Sir Peter Chalmers Mitchell has added not a little to the considerable indebtedness which all zoologists already owe him by preparing this history of the first hundred years of the existence of the Zoological Society of London. It is entertainingly written, and at the same time a valuable contribution to the records of the history of science. The Zoological Society may well be proud of its record of achievement. Its publications have uniformly maintained a very high standard of excellence; its Zoological Garden in Regent's Park has long been the world model for such institutions; and in keeping up the publication of the *Zoological Record* a service of inestimable value to the progress of systematic zoology has been performed. With an annual income running at present above $700,000 a year and likely to increase, the future looks bright. We feel certain that all American zoologists will join with us in congratulating the Society and its efficient Secretary on its achievements and its prospects.

FAUNE ENTOMOLOGIQUE DE LA PROVINCE DE QUÉBEC. *Vol. IV. Sixième Ordre. Les Lépidoptères. Fascicule I. Diurnes.*
By l'Abbé L. Provancher and le Chanoine V.-A. Huard. *Franciscaine Missionnaire*
$1.00 *Quebec*
6¼ x 9¼; xi + 101 (paper)

This fascicle, published in 1929, is the continuation of an enterprise begun in 1877. It gives directions for collecting and mounting butterflies, followed by systematic descriptions of the diurnal species which have been recorded in Quebec. The rather infrequent illustrations are not very successful, being mostly muddy and blurred half-tones in the text.

DIE NEDERLANDSCHE BEEK-TRICLADEN EN DE OORZAKEN VAN HAAR VERSPREIDING.
By A. D. Voûte.
Zuid-Hollandsche Boek- en Handelsdrukkerij
6 shillings *'s-Gravenhage*
6¼ x 9¼; 116 (paper)

A doctoral dissertation on the local distribution of planarians in Holland, considered from the ecological and behavioristic viewpoints. The author concludes that neither *Planaria alpina* nor *Polycelis cornuta* can be regarded as glacial-period relicts in their Dutch habitats.

PRINCIPLES OF FOREST ENTOMOLOGY.
By Samuel A. Graham.
McGraw-Hill Book Co., Inc.
$3.50 5¾ x 9; xiv + 339 *New York*

As its name implies this is not a handbook of all the species of insects that feed on trees, but a well written discussion of

the relations between forest insects and their environment and of the bearing of these principles on problems of insect control in forestry. In his treatment the author uses Chapman's concepts of biotic potential—the ability of a species to multiply in a given time when placed under the most favorable conditions—and environmental resistance—the sum of all the factors in an environment that tend to reduce the rate of insect multiplication. As the biotic potential is constant for a given species it follows that if any factor in the environmental resistance decreases without a compensating increase in other factors, the biotic balance is upset and the species may become epidemic. Control operations are then necessary to restore the environmental resistance to its former level. The book discusses in detail the various methods of control and the various ecological groups of forest insects with examples taken from the more important pests.

SCIENCE OF THE SEA. *An Elementary Handbook of Practical Oceanography for Travellers, Sailors, and Yachtsmen.*
Prepared by the Challenger Society for the Promotion of the Study of Oceanography. Originally edited by G. Herbert Fowler. Second Edition edited by E. J. Allen.
Oxford University Press
$6.00 $5\frac{3}{4}$ x $8\frac{7}{8}$; xxiii + 502 *New York*

"Not seldom those who are engaged in oceanographic work are asked by some one about to start on a long voyage: 'How can I do some work for science? I don't know anything about it; where can I "read it up"?'" This book, designed to give the needful information to such amateurs, has set at least one reader wild to go on an oceanographic expedition of his own. We note that Professor D'Arcy Thompson thinks there is something in the sea-serpent.

THE COWBIRDS. *A Study in the Biology of Social Parasitism.*
By Herbert Friedmann. *Charles C. Thomas*
$6.00 net *Springfield, Ill.*
$6\frac{1}{2}$ x $9\frac{1}{2}$; xvii + 421

This is a contribution of first rate importance to natural history, ecology, animal behavior and evolution. The book is extensively and well illustrated by original photographs. It is beautifully printed and does great credit to the publisher as well as the author.

Five years of study in central New York, in Argentina, and on the Texan-Mexican border have yielded Dr. Friedmann a rich harvest of knowledge of the natural history of the Cowbirds and especially of nest parasitism, a habit which they share with the cuckoos and a few other forms. His conclusion is that "the immediate cause of the origin of the parasitic habit in the Cowbirds was the loss of the protecting instinct of the male." There is a bibliography of 36 pages.

COMPARATIVE ZOOLOGY. *An Introduction to the Study of Comparative Anatomy, Comparative Embryology and Taxonomy.*
By Cecil von Bonde. *Juta and Co., Ltd.*
21 shillings *Capetown*
$5\frac{1}{4}$ x $8\frac{3}{4}$; v + 240

A text book in which the divisions are I. Comparative Anatomy; II. Comparative Embryology; III. Taxonomy.

ANIMAL PARASITOLOGY. *With Special Reference to Man and Domesticated Animals.*

By Robert Hegner, Francis M. Root and Donald L. Augustine. *The Century Co.*

$6.50 $5\frac{3}{4}$ x $8\frac{3}{4}$; xxi + 731 *New York*

This encyclopedic textbook consists of an introduction on Parasitism in Animals and a section on Protozoology by Hegner, and sections on Helminthology by Augustine and on Medical Entomology by Root. The parasites of man are emphasized, and those of domestic animals are described whenever possible. There is a bibliography of 57 pages and author and subject indexes.

A TEXTBOOK IN GENERAL ZOOLOGY.

By Henry R. Linville, Henry A. Kelly and Harley J. Van Cleave. *Ginn and Co.*

$1.80 $5\frac{1}{8}$ x $7\frac{1}{8}$; viii + 463 *Boston*

A revision by Van Cleave of Linville and Kelley's *Textbook in General Zoology*. It is designed as the basis for a full year's course for students beginning the subject. In the revision an attempt has been made to give a distinct biological orientation of the subject. The book is interestingly written and well illustrated.

BOTANY

LEAF TEMPERATURES OF COTTON AND THEIR RELATION TO TRANSPIRATION, VARIETAL DIFFERENCES, AND YIELDS. *United States Department of Agriculture Technical Bulletin No. 91.*

By Frank M. Eaton and Galen O. Belden.

U. S. Government Printing Office

10 cents *Washington*

$5\frac{3}{4}$ x $9\frac{1}{8}$; 40 (paper)

Thermo-electric measurements show differences among cotton varieties in departure of the leaf temperature from the temperature of the air. The variety with high leaf temperatures has shown poor yields in years with high summer temperatures, whereas the variety with lower leaf temperatures has shown no such relation.

THE GENUS HAPLOPAPPUS. *A Phylogenetic Study in the Compositæ. Carnegie Institution of Washington Publication No. 389.*

By Harvey M. Hall. *Carnegie Institution*

$5.00 *Washington*

$6\frac{7}{8}$ x 10; viii + 391 (paper)

A taxonomic monograph attempting to classify a group of plants on the basis of their probable course of evolution. The author depends not only on field and herbarium studies but on experimental transplantation of diverse forms into a uniform environment. The conclusion is drawn that

> the species of North America have become definitely separated from those of farther south and that within each group there has been a development and differentiation which has led to the separation of smaller groups sufficiently distinct to be recognized as sections, 16 of these being in the north, 5 in the south. The nearest approach between sections appears to be between *Blepharodon* and *Euhaplopappus*, but even here the separation is based upon good technical grounds. It seems impossible, however, to set up any single character for the separation of all sections of North America from all those of South America, chiefly because of the numerous combinations in which the characters occur. It is for this reason that the primary geographic groups are not formally designated as subgenera.

ORGANOGRAPHIE DER PFLANZEN. *Insbesondere der Archegoniaten und Samenpflanzen. Erster Teil. Allgemeine Organographie.*
By K. Goebel. *Gustav Fischer*
30 marks (paper) *Jena*
32 marks (cloth)
7 x 10¼; ix + 642

Goebel's *Organographie* is one of the great classics of biology. The first, general, part has long been out of print and this new third edition is therefore very welcome. The material has been thoroughly revised and brought up to date, additions having been made to practically all sections. A further long period of usefulness lies before the book.

DIE KLIMATEN DES ERDBALLS UND DIE CHEMISCHE TÄTIGKEIT DER PFLANZEN.
By Sergius Ivanow. *Urban und Schwarzenberg*
4 marks 7 x 10; 39 (paper) *Berlin*

The point brought out in this number of the *Fortschritte der Naturwissenschaftlichen Forschung*, edited by Abderhalden, is that plants exhibit geographical variation in respect of their chemical constitution. This fact cannot be regarded as an entirely novel contribution, but the author brings a wealth of detail to its support, largely derived from his own studies of oil bearing plants in various parts of Russia and Siberia. The pamphlet is a curious and occasionally amusing mixture of sound and useful scientific information with Chamber of Commerce babbittry. The author lectures the Soviet Government at length about what they must do to promote a sound linseed oil industry for Russia.

LES PLANTES ALIMENTAIRES CHEZ TOUS LES PEUPLES ET À TRAVERS LES AGES. HISTOIRE, UTILISATION, CULTURE. *Volume II. Phanérogames Fruitières.*
By D. Bois. *Paul Lechevalier*
80 francs 6½ x 10; 638 (paper) *Paris*

This second volume, which completes Prof. Bois' valuable treatise on domesticated food plants, deals with the plants bearing edible fruits. It contains a wealth of information, covering a wide range beyond the directly botanical. It is copiously illustrated with line drawings, and will form a useful reference work in the agricultural and botanical fields. There is a detailed index.

LA VIE DE LA CELLULE VÉGÉTALE. *Les enclaves de la matière vivante.*
By Raoul Combes. *Armand Colin*
9 francs *Paris*
4½ x 6¾; 220 (paper)

The second volume in a planned trilogy on the plant cell. The first volume was noticed in this REVIEW earlier (Vol. III, p. 296). The present volume is devoted to the subject of the vacuoles in plant cells, and their contents. It is a well-written, valuable book. The author is an uncompromising mechanist, bitterly opposed to the slightest and most innocent implication of teleology in biological discussion. He goes so far as to say that glycogen should not be called a "reserve substance," because to do so implies that the organism has an end in view. Rather glycogen should be called "a form of accumulation" of glucides. Such meticulous verbalism leaves us cold, though we appreciate the spirit which so stiffens one's backbone.

PLANT SUCCESSION AND INDICATORS. *A Definitive Edition of Plant Succession and Plant Indicators.*
By Frederic E. Clements.
The H. W. Wilson Co.
$8.50 6¾ x 9¾; xvi + 453 *New York*

This is a combined and condensed edition of the author's *Plant Succession* and *Plant Indicators* published in 1916 and 1920 by the Carnegie Institution of Washington. The portions of the original editions here omitted are to form the nuclei of three books, dealing with studies of succession in North America and Eurasia, with the new field of paleo-ecology, and with the climax formations of western North America.

The fundamental concept underlying Clements' work is that the unit or climax formation is an organic entity, which arises, grows, matures, and dies, whose "response to the habitat is shown in processes or functions and in structures which are the record as well as the result of those functions," and which is able to reproduce itself. All these are characteristic attributes of organisms. Clements traces the development of a sere or succession from a bare area, produced by various initial causes, through stages of migration of plants into the bare area, of adjustment and competition there, and of stabilization, to the climax stage, where "the occupation and reaction of a dominant are such as to exclude the invasion of another dominant." The second part of the book is built on the concept of plants, and especially plant communities, as indicators of soil and climate and therefore of the behavior of other plants and of animals in the same spot. There is a bibliography of 16 pages but no index.

This is an important ecological work, which fits in very neatly from the botanical side with Wheeler's concept of the society as the next emergent above the individual.

DEUX ÉPIBIOTES REMARQUABLES DE LA MINGANIE. *Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 12.*
By Frère Marie-Victorin. Laboratoire de Botanique, Université de Montréal
50 cents *Montreal*
6 x 9; 14 + 4 plates (paper)

LE DYNAMISME DANS LA FLORE DU QUÉBEC. *Essai sur les forces d'évolution et d'élimination en oeuvre dans certaines populations végétales. Contributions du Laboratoire de Botanique de l'Université de Montréal—No. 13.*
By Frère Marie-Victorin. Laboratoire de Botanique, Université de Montréal
$1.00 6 x 9; x + 89 (paper) *Montreal*

The first of these monographs deals with *Cypripedium passerinum* var. *minganese* and *Draba luteola*. The second is an interesting essay on ecological aspects of evolution. The author discusses especially the effect of man's activity on the flora of the earth, comparing its tendency to produce uniformity to the levelling effect of erosion.

FIELD BOOK OF AMERICAN WILD FLOWERS. *Being a Short Description of Their Character and Habits, a Concise Definition of Their Colors, and Incidental References to the Insects Which Assist in Their Fertilization.*
By F. Schuyler Mathews.
G. P. Putnam's Sons
$3.50 4 x 6¾; xxxii + 558 *New York*

A revised edition of a popular field book covering the flowering species of the east-

ern United States. A color key to assist in the identification of specimens as well as a family key and a general index are provided.

THE GIANT CACTUS. *God's Monument to Faith, Patience and Perseverance.*
By Grace P. Nickerson. Trade Printing Co.
$1.00 $6\frac{1}{4}$ x $10\frac{1}{8}$; 29 *Los Angeles*

A brief, superficial but extremely enthusiastic account of these curious creatures of nature.

DIE LEBENSDAUER DER PFLANZE.
By Hans Molisch. *Gustav Fischer*
7.50 marks (paper) *Jena*
9 marks (bound)
$6\frac{3}{4}$ x $10\frac{1}{8}$; viii + 168

An excellent and much needed treatise on the biology of life duration in plants, by the distinguished plant physiologist of Vienna. After an introductory chapter on duration of life, in general, in plants there are discussed means of prolonging the life of plants; rejuvenescence; latent life (*Scheintod*) in plants; and senescence, death and potential immortality of trees. There are author and subject indices. This will be a valuable reference work for all students of duration of life and related problems.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 300.* Containing following articles: *Vom Sammeln und Präparieren der Kieselalgen sowie Angaben über Untersuchungs- und Kulturmethoden*, by Friedrich Hustedt; *Methoden zur Untersuchung der Kohlensäureassimilation*, by Hans Gaffron; *Methoden zum Nachweis pflanzlicher Wundhormone*, by Walter Kotte; *Neuere Methoden zur Ermittlung des Offnungszustandes der Stomata*, by M. G. Stalfelt.
Urban und Schwarzenberg
10 marks 7 x 10; 192 (paper) *Berlin*

Of general interest to botanists this number of the Abderhalden *Handbuch* contains, as its first article, the best account we have seen of all aspects of the technique of studying living diatoms.

AGRICULTURAL AFGHANISTAN (*Composed on the basis of the data and materials of the Institute of Applied Botany to Afghanistan.*)
By N. I. Vavilov and D. D. Bukinich.
Institute of Applied Botany and State Institute of Experimental Agronomy
12 rubles 7 x $10\frac{1}{8}$; 610 + xxxii *Leningrad*

A detailed report in Russian, with an extended summary in English, of an agricultural exploring expedition into Afghanistan, under the direction of the distinguished geneticist, Prof. Vavilov. Over 7000 samples of cultivated plants were collected, and tested out during three consecutive years in various parts of Russia. There are over 300 illustrations. These and the English summary are so interesting as to make one long to be able to read Russian, to get more of the details of this notable piece of biological exploration.

TREES AND SHRUBS OF MINNESOTA.
By Carl O. Rosendahl and Frederic K. Butters.
University of Minnesota Press
$4.00 *Minneapolis*
$6\frac{3}{4}$ x 10; viii + 385

A book which will give much pleasure to all those interested in the woody plants to be found not only within the boundaries

of Minnesota but in the vast area extending from the Great Lakes to the Rocky Mountains. The authors have done their work with extraordinary care. Although designed primarily as a guide for the amateur and non-professional botanist the book meets all of the requirements of the serious student. Much material has been taken from the earlier work *Minnesota Trees and Shrubs* but the present volume is not simply a second edition of that treatise. It deals with native and introduced forms to the number of 47 families, 107 genera, 324 species, 40 varieties, 14 forms and 18 hybrids. The arrangement of families is according to the Englerian System, while in questions of nomenclature the International Rules as set forth by the Vienna Congress of 1905 and revised by the Brussels Congress of 1910 have been followed. An introductory chapter and glossary furnish the amateur with the necessary technical information. The book is beautifully printed and excellently illustrated with 250 figures and plates.

THE SCIENTIFIC PRINCIPLES OF PLANT PROTECTION.
By Hubert Martin. Longmans, Green and Co.
$8.40 5¾ x 8½; xii + 316 *New York*

The primary object of this book is to make "a comprehensive survey of the scientific principles underlying modern methods of control of crop pests" as an aid in the ever increasing necessity for cooperation between the entomologist or mycologist, on the one hand, and the chemist, physicist or plant physiologist, on the other. The author deals clearly and in detail with the diverse aspects of the problem: chemical and physical modes of attack by fumigating or spraying with insecticides or fungicides; the treatment of soil and seed by chemicals; the use of insects, fungi or bacteria as enemies of plant parasites; selecting and breeding disease resistant strains; etc. The book is well documented and has author and subject indices.

THE HYDROSTATIC-PNEUMATIC SYSTEM OF CERTAIN TREES: MOVEMENTS OF LIQUIDS AND GASES. *Carnegie Institution of Washington Publication No. 397.*
By D. T. MacDougal, J. B. Overton and Gilbert M. Smith. Carnegie Institution
$1.25 *Washington*
6⅞ x 10; 99 (paper)

A further report on the important experimental researches of MacDougal and his associates on the movement of water in trees. The first conclusion reached is that: "Our experiments show that the living cells of the stem have no active rôle in sap-flow other than their effect upon the osmotic concentration of the transpiration stream." This volume is a contribution of first rate importance to the literature of plant physiology.

MORPHOLOGY

VERGLEICHENDE ANATOMIE DES NERVENSYSTEMS DER WIRBELLOSEN TIERE. *Unter Berücksichtigung Seiner Funktion.*
By Bertil Hanström. Julius Springer
76 marks (paper) *Berlin*
78.60 marks (cloth)
7 x 10; xi + 628

A thorough, detailed, and comprehensive review of the existing knowledge of the nervous system in invertebrates, with a strong flavor of emphasis on the functional aspects throughout. The book is

abundantly and well illustrated; is thoroughly documented, though it is questionable if it would not have been more practically useful to have collected together in one place all the bibliographies which are scattered through the book after each chapter; and is fairly well indexed. It constitutes a valuable reference work in its field.

ENTWICKLUNGSGESCHICHTE DES MENSCHEN *mit Berücksichtigung der Wirbeltiere.*

By Richard Weissenberg. Originally by L. Michaelis. *Georg Thieme*
10.70 marks *Leipzig*
$5\frac{1}{8}$ x $7\frac{3}{4}$; xii + 293 + 6 plates

So successful has this handbook of human embryology been that Professor Weissenberg now issues a new and enlarged eleventh edition, with his name appearing as the primary author. Within its brief limits it is one of the best available summaries of what is known about the embryonic development of the vertebrate body in general and the human body in particular. It is well illustrated and indexed.

COMPARATIVE NEUROLOGY. A *Manual and Text for the Study of the Nervous System of Vertebrates.*

By James W. Papez. *Thomas Y. Crowell Co.*
$6.00 $5\frac{3}{4}$ x 9; xxv + 518 *New York*

An introductory laboratory course divided into three parts: I. Gross Structure of the Brain of Mammals; II. Microscopic Structure of the Mammalian Nervous System; III. Brains of Lower Vertebrates. It is amply supplied with diagrammatic drawings and contains lists of references.

COMPTES RENDUS DE L'ASSOCIATION DES ANATOMISTES. *Vingt-troisième Réunion (Prague, 2–4 avril 1928). Edited by Remy Collin.*

L'Association des Anatomistes,
11 francs in France *Faculté de Médecine*
12 francs in foreign countries *Paris*
$6\frac{1}{2}$ x $9\frac{3}{4}$; lii + 559 (paper)

This volume of the proceedings of the 1928 meeting of the French Association of Anatomists contains some 91 papers, many of real interest and novelty, besides the minutes of the meeting.

LEHRBUCH DER ENTWICKLUNG DES MENSCHEN.

By Alfred Fischel *Julius Springer*
86 marks (paper) *Berlin*
88.80 marks (bound)
$6\frac{3}{4}$ x $10\frac{1}{8}$; viii + 822

A detailed and thorough textbook of human embryology, extensively and beautifully illustrated. It is a textbook in the strictest sense. There are no bibliographical citations whatever, except that borrowed figures are credited to the original author, but without citation of place of publication. Here is set down, in excellent order and thoroughness of detail, that which needs to be learned by the student of the development of the human body. The book is well indexed. But indubitably its value as a *reference* work is diminished by the absence of a bibliography.

A COURSE IN COMPARATIVE ANATOMY. In four volumes, as follows: *Outline Lectures in Comparative Anatomy and Vertebrate Zoölogy; The Dissection of the*

Dogfish; The Dissection of the Turtle; The Dissection of the Toad with Remarks on the Anatomy of the Frog and the Salamander. *By Edwin C. Starks and Lot D. Howard.* *Stanford University Press*

$3.00 per set *Stanford University*

6 x 8¾; I, 49 (paper)
II, 36 (paper)
III, 36 + 2 plates (paper)
IV, 34 + 2 plates (paper)

A didactic outline of lectures for an elementary course in comparative anatomy and three laboratory manuals for the dissection of the dogfish, turtle and toad. There is a short list of references supplied with each part.

ÉLÉMENTS D'HISTOLOGIE. *I. Cellule. Division cellulaire. Différenciation cellulaire. Classification morphologique et fonctionnelle des cellules, tissus et organes. Éléments de soutien, contractiles, nutritifs. Sang, lymphe, organes hématopoiétiques, vaisseaux sanguins et lymphatiques.* *By P. Bouin.* *Félix Alcan*

120 francs *Paris*

8⅝ x 10⅝; vii + 334

This first volume of a new and comprehensive textbook of histology, by the great French master in that field, Professor Bouin, is concerned with the cell in general, the problem of differentiation, and cell physiology. The orthodox plan of arranging treatises on histology on the basis of tissues and organs is here wholly abandoned, and replaced by the more logical plan of treating together those basic cellular elements which play a common rôle. The whole outlook of the book is fresh and stimulating. It is beautifully printed and illustrated. Following each chapter is a selected, but rather extensive, bibliography. The whole work, when completed, will take rank as a standard text and reference book.

CONTRIBUTIONS TO EMBRYOLOGY. *Volume XX, Nos. 109 to 117. Publication No. 394.*

Carnegie Institution of Washington

$5.50 (paper) *Washington*

$6.50 (cloth)

9 x 11¾; 257

This volume contains the following contributions: Early stages in the development of pig embryos, from the period of initial cleavage to the time of the appearance of limb-buds, by C. H. Heuser and G. L. Streeter; The development of the meninges in amphibia: a study of normal and experimental animals, by Louis B. Flexner; On the placentation of primates, with a consideration of the phylogeny of the placenta, by G. B. Wislocki; A well-preserved human embryo of 10 somites, by George W. Corner; The topographic history of the volar pads (walking pads; *Tastballen*) in the human embryo, by Harold Cummins; A correlated study of the development of reflex activity in fetal and young kittens and the myelinization of tracts in the nervous system, by Orthello R. Langworthy; The effect of various solutions and salts on the pulsation rate of isolated hearts from young chick embryos, by Warren H. Lewis; Macrophages and other cells of the deep fascia of the thigh of the rat, by Warren H. Lewis; The technique of measuring the outer body of human fetuses and of primates in general, by Adolph H. Schultz.

The usual high standard of excellence associated with the work of the Carnegie Institution Department of Embryology is well maintained in this volume, both as to matter and method of presentation.

PHYSIOLOGY AND PATHOLOGY

THE COMPARATIVE PHYSIOLOGY OF MUSCULAR TISSUE.
By A. D. Ritchie. *The Macmillan Co.*
$3.00 5½ x 8½; xi + 111 *New York*

A valuable contribution to this special field. There are four general headings: General characters of muscular tissue; chemical changes in active muscle; mechanics and theory of muscular contraction; and effect of environment. The author is led by his own researches and an extensive review of the literature to the conclusion that so far as evidence goes the mechanism underlying the simple muscle twitch is sufficient to explain all muscle processes. The difference between muscles seems to be in the speed of the processes rather than in their quality. The book is well documented and indexed.

A REPORT OF EXPERIMENTS INDICATING SOME NEW FACTORS IN RESPIRATION. *University of Toronto Studies. Physiological Series No. 98.*
By E. Fidlar. *University Library*
50 cents 6¼ x 9¾; 77 (paper) *Toronto*

The detailed report of an extremely interesting and ingenious piece of physiological research, leading to the conclusion that in the respiration of frogs in a closed circuit there is evidence of "the presence of unknown gas or gases, assumed 'nitrogen,' not only as an excretion of the animal, but also as an absorption, and in the two most accurate experiments the ratio of outgo to uptake was about 2:1."

WHEAT FLOUR AND DIET.
By C. O. Swanson. *The Macmillan Co.*
$2.50 4⅞ x 7⅜; xiii + 203 *New York*

This book is written for the general reader. Teachers of home economics, diet and nutrition, and milling processes, however, will find it useful. Its aim is to give, in non-technical language, the different operations involved in the complex process of making wheat flour. In addition, there is an account of the development of the milling industry, which had its origin long before written history, a chapter on vitamines, and a discussion of the importance and uses of the various types of wheat. Considerable space is devoted to the value of wheat flour in the diet and to the general relations of food to health. This latter part is particularly sound and satisfying when one considers the great mass of half-baked and dubiously seasoned food-lore which of late has been so frequently dished up for the general reader's diet. The illustrations are well chosen.

DAS PERMEABILITÄTSPROBLEM. *Seine Physiologische und Allgemeinpathologische Bedeutung.*
By Ernst Gellhorn. *Julius Springer*
34 marks (paper) *Berlin*
35.40 marks (cloth)
5¾ x 8¾; x + 441

A useful critical review of the literature, to the middle of the year 1928, on permeability, together with some original experimental work of the author in this field, not published elsewhere. The bibliography is colossal, running to about 1400 titles. The main topics discussed are the methodology of experimental work on permeability; the permeability of the cell; and the permeability of organs. These sections are followed by a general summary and synthesis of results.

LA VACCINATION ANTITUBERCULEUSE AVEC LES BACILLES VIVANTS CHEZ LES ANIMAUX ET CHEZ L'HOMME. *By Alberto Ascoli, in collaboration with E. Gentili, G. Gerosa, A. Mangiarotti, D. Nai, C. Setti, F. Omodeizorini.*

Istituto Editoriale Cisalpino

$6\frac{1}{4}$ x $9\frac{1}{8}$; iii + 235 (paper) *Milano*

An account of the author's own researches, with a historical setting, and much discussion of Calmette's BCG work. The book is chiefly of interest to the clinician and public health worker, rather than the biologist. It unfortunately lacks an index.

FOOD, NUTRITION AND HEALTH. *By E. V. McCollum and Nina Simmonds.*

E. V. McCollum

East End Post Station Box 25,

$1.60 $4\frac{7}{8}$ x $7\frac{1}{2}$; vii + 148 *Baltimore*

A revised second edition of a popular treatise on the results of modern research on food and nutrition. The book contains much that is sound and interesting, especially in those chapters dealing with the vitamines. Its greatest value is perhaps to a somewhat specialized group—the physician, the dentist, the dietitian and the nurse. As no modern popular treatise of this kind is complete without aids to reducing or increasing the body weight, so we find the latter third of the book devoted to such suggestions, together with a "system of diet promoting health."

TRACKING DOWN THE ENEMIES OF MAN. *Being the Romance of a Doctor's Life in the Jungles.*

By Arthur Torrance. J. H. Sears and Co., Inc.

$3.50 $5\frac{1}{2}$ x $8\frac{1}{8}$; xiii + 296 *New York*

This somewhat lurid book is launched by Trader Horn and Morris Fishbein. It recounts various adventures of the author in the course of his medical service and experience in the tropics. It is highly entertaining reading though of no scientific significance.

DIE MALARIA *in ihrer Bedeutung für die Geschichte Roms und der römischen Campagna. Eine kulturhistorische Studie.*

By Angelo Celli (Edited by Anna Celli-Fraentzel, with a foreword by Henry E. Sigerist). *Georg Thieme*

12 marks *Leipzig*

$6\frac{1}{2}$ x $9\frac{3}{4}$; vi + 118 (paper)

It is a real service to have this renowned essay of Celli available in German. It is a thorough historical study of the epidemiology of malaria in the Roman *campagna*, thoroughly documented, and makes a fundamental contribution to human biology in general, as well as to epidemiology in particular.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 288.* Containing following articles: *Ein transportabler Respirationsapparat für medizinische, anthropologische und andere wissenschaftliche Expeditionen: Ein einfacher adiabatischer Calorimeter zur Bestimmung der Energiewerte von Brennstoffen, Nahrungsmitteln und Exkreten;* and *Der Oxycalorimeter,* by Francis G. Benedict.

Urban und Schwarzenberg

4 marks 7 x 10; 80 (paper) *Berlin*

Lieferung 293. Methoden und Technik der Nerven- und Muskelphysiologie bei wirbellosen Tieren.

By H. J. Jorden and P. J. van der Feen

Urban und Schwarzenberg

8 marks 7 x 10; 143 (paper) *Berlin*

Lieferung 296. Containing the following articles: *Methoden zur experimentellen*

Schädigung des Gehörorgans durch Schalleinwirkung, by Carl v. Eicken; *Elektrische Methoden zur Klanganalyse*, by Ferdinand Trendelenburg.

Urban und Schwarzenberg

6 marks 7 x 10; 99 (paper) *Berlin*

These three numbers of the Abderhalden *Handbuch* are of special interest to physiologists. The first by Dr. Benedict, director of the Carnegie Institution's Nutrition Laboratory, is especially important because it describes extremely neat and compact pieces of apparatus, by means of which metabolism may be studied in the field.

ÉTUDE ÉLÉMENTAIRE DES ARYTHMIES. *Lecture des Éléctrogrammes Phono et Cinématographie.*

By R. Lutembacher. *Masson et Cie*

30 francs *Paris*

$7\frac{3}{8}$ x $10\frac{1}{2}$; 110 (paper)

A beautifully illustrated treatise on electrocardiography, with especial reference to pathological disturbances of the cardiac rhythm. The different common cardiac lesions are discussed and electrocardiograms illustrating them are reproduced. There are also examples of microcinematography.

FUNGI AND FUNGOUS DISEASES (*Adolph Gehrmann Lectures of the University of Illinois College of Medicine 1926*).

By Aldo Castellani. *American Medical Assoc.*

$1.50 $6\frac{7}{8}$ x 10; 203 (paper) *Chicago*

Three lectures by the noted authority on Tropical Diseases: I. Fungi; II. Fungous Diseases; III. Skin Diseases Due to Fungi.

NOMENCLATURE *of Diseases and Operations and Manual of the Medical Record.*

By T. R. Ponton. *Physicians' Record Co.*

$3.50 $6\frac{1}{4}$ x $9\frac{1}{2}$; 199 *Chicago*

Alphabetical list of some 24,000 diseases according to a nomenclature approved by the American College of Surgeons and the American Hospital Association. Each disease has a number for use in punch card index systems, and a letter designation to facilitate the assignment of cases to different hospital departments. There are also a list of surgical operations and sample hospital records.

THE GENESIS OF EPIDEMICS *and The Natural History of Disease. An Introduction to the Science of Epidemiology Based upon the Study of Epidemics of Malaria, Influenza, and Plague.*

By Clifford A. Gill. *William Wood and Co.*

$7.50 $5\frac{3}{4}$ x 9; xxvi + 550 *New York*

This is an exceedingly well reasoned inquiry into the basic nature of the etiology of epidemics. The author, who is Director of Public Health in the Punjab, has had an extensive experience with epidemic disease in the field and tells of the origin of the present work. Having been engaged in the study of malaria in the Punjab continuously from 1913 to 1923 and for some years again after an interruption by the war, he published a definitive paper in 1921 stating provisionally the hypothesis which appeared to him to account for the malarial outbreaks. Later, taking up other epidemics for their bearing on his malarial work he was impressed with the similarity of all epidemical phenomena and in 1922 a generalization applicable to all epidemics of disease was adopted. It is thus seen that the author's theory has the merit of having been inductively developed, and

following this it was tested by application to influenza, plague, and certain other diseases with such satisfactory results that a complete synthesis was undertaken.

The presentation is arranged in five parts. The first, an introductory one, defines an epidemic as a sharp increase in incidence over a short period of time, and epidemicity is defined dynamically to refer to "those qualities affecting the seed and the soil whereby certain diseases are enabled periodically to exhibit epidemical phenomena." It then recounts the previous views regarding the cause of epidemics, outlines the objects of epidemiological research and gives a brief statement of the author's theory of the genesis of epidemics. Part II is devoted to the results of an investigation of epidemic malaria and an account of studies of influenza and plague. Part III is an analysis of an application of the author's theory of epidemics. Part IV contains a discussion of the influence of evolutionary factors on disease and the effect of climate. Part V is a review and reflects on the implications of the author's views for the theory and practice of preventive medicine.

Colonel Gill calls his hypothesis the "quantum theory," and it is a generalization applying to all epidemics in spite of the apparent disparate character of epidemics of different diseases. Instead of attributing epidemics to changes in an individual factor, such as the biological modification of the specific parasite, which is the prevalent view, the author proposes the idea that they arise as a result of the disturbance of a quantitative equilibrium between toxin and degree of immunity. A number of influences may bring about such a disturbance and four factors are emphasized: (1) the reservoir of infection, (2) the parasite factor, (3) the immunity factor, and (4) the transmission factor. The factor of predominating importance is the one of transmission, and this in turn is largely affected by meteorological conditions. The theory is presented with great skill, and much evidence, which there is no space available here to review, is educed in its favor. Whether or not it eventually stands, Colonel Gill has produced a great work on epidemiology as lucidly written as it is well conceived.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 287.* Containing following articles: *Sulfonieren,* by Josef Halberkann and Fritz Fretwurst; *Biologisch wichtige Reaktionen und Reagenzien,* by Eduard Strauss and Karl Koulen.

Urban und Schwarzenberg
10 marks 7 x 10; 180 (paper) *Berlin*

Lieferung 294. Darstellung metallorganischer Verbindungen.
By Emil Klarmann. Urban und Schwarzenberg
8 marks 7 x 10; 158 (paper) *Berlin*

Lieferung 299. Halogenieren.
By Hugo Bauer. Urban und Schwarzenberg
14 marks 7 x 10; 276 (paper) *Berlin*

The articles in these three numbers of the great Abderhalden *Handbuch* are chiefly of interest to biochemists. The one by Strauss and Koulen on biologically important reactions and reagents is of general biological interest and usefulness.

THE CHEMICAL ACTION OF ULTRA-VIOLET RAYS.
By Carleton Ellis and Alfred A. Wells.
The Chemical Catalog Co., Inc.
$6.50 6 x 9; 362 *New York*

A summary and not very searching

account of some of the chemical and biological uses of ultra-violet radiation.

ENZYME ACTIONS AND PROPERTIES.
By Ernst Waldschmidt-Leitz. Translated and Extended by Robert P. Walton
John Wiley and Sons, Inc.
$4.00 net *New York*
$5\frac{3}{4}$ x 9; xviii + 255

"The material within this volume constitutes a general treatment of enzyme action and properties as interpreted principally from the viewpoint of the Willstätter school. Prof. E. Waldschmidt-Leitz, the active associate of R. Willstätter, has given a condensed description of the most important principles of enzyme chemistry and of the special characteristics of the most prominent enzymes. The work has not been attempted as an exhaustive compendium of enzyme literature but rather as a concise presentation of the most fundamental principles and best accepted characteristics of enzyme action."

THYROXINE.
By Edward C. Kendall.
The Chemical Catalog Co., Inc.
$5.50 6 x 9; 265 *New York*

The scope of this monograph, the forty-seventh in the authoritative series issued by the American Chemical Society, is indicated by the following extracts from the preface.

What has been assembled in the monograph has been chosen from the viewpoint of a chemist and with a desire to correlate the activity of the thyroid gland with reactions which involve oxidation. . . .

The theoretical deductions in this monograph have been largely based on three contributions: the clinical classification of goiter and the use of iodine in exophthalmic goiter which have been suggested by Plummer: the isolation of thyroxine from the gland; and the extensive studies in basal metabolism and nitrogen metabolism in relation to thyroxine and thyroid diseases which have been carried out by Boothby and his coworkers. . . .

The experimental results to which reference has been made have been limited to those that establish the physiologic activity of thyroxine and those necessary to relate the action of the thyroid gland to the normal physiology of the human being.

SEX

A RESEARCH IN MARRIAGE.
By G. V. Hamilton.
Albert and Charles Boni, Inc.
$10.00 6 x 9; xiii + 570 *New York*
WHAT IS WRONG WITH MARRIAGE.
By G. V. Hamilton and Kenneth MacGowan.
Albert and Charles Boni, Inc.
$3.00 $5\frac{1}{2}$ x $8\frac{5}{8}$; xxi + 319 *New York*

The investigation of sex life and marriage which forms the basis of these two books deserves attention and commendation as a pioneer effort in an important but too much neglected field of human biology. It is easy to criticise specific weakness in Dr. Hamilton's work, and this has been rather freely done. But really pioneer work in any field of science is only rarely perfect.

Dr. Hamilton, in the following statement, makes clear in general terms the nature of his material and of the investigation as a whole.

An almost freakish combination of circumstances made it possible for me to obtain intimate and extensive self-revelations from two hundred married persons who are serious-minded, more or less importantly occupied and well above the average as to intelligence and cultural attainment. At least half of them could be rated as "normal" in the sense that their spousal, parental, social and vocational adjustments conform to standards which are not exceeded by the majority of Americans. Nevertheless, it would be over-optimistic to say that as many as five per cent of them

have escaped more or less serious damage by preventable things which were done to them during childhood. This book presents (1) some of the more important things that happened to the two hundred spouses of my study during their childhood, and (2) their present beliefs, attitudes, predicaments, and characteristic modes of performance with reference to sex and marriage. It is therefore in a measure a study of the child in the adult.

The actual technique was, in briefest outline, to place each subject in a comfortable chair in Dr. Hamilton's office and present the person with library cards, one by one, on each of which was typed one or more questions about their sex life, in nearly all the aspects conceivable. Dr. Hamilton sat quietly at his desk and wrote down the answers, as they were freely "talked out."

The book is devoted to detailed compilations (or really lists in many cases) of the answers to these questions. Quite intentionally, whether wisely or not, the result is of the nature of a large collection of trees, rather than a forest. Dr. Hamilton is very modest throughout, and refrains from drawing any general conclusions. In spite of the inevitable defects of a first trial the book is a notable contribution.

The second book is a popular presentation of some of the material, for general circulation. The *Research in Marriage* is prohibited from circulation except among the members of certain professions.

THE INVERT *and his Social Adjustment. By Anomaly.* *The Williams & Wilkins Co.*
$2.00 4 x 6½; xxxii + 160 *Baltimore*

This interesting little book may be described as a sort of handy guide or *vade mecum* for the homosexual desirous of keeping out of jail. These unfortunate persons have a difficult time adjusting themselves in a world run by and for heterosexuals. The author is a Roman Catholic, and has derived help from that source in his difficulties. He ends on an optimistic note. "I predict that the next decade will witness a better understanding of the facts of inversion by all educated people, and better understanding will relieve inverts from much of the present necessity for dissimulation."

On the whole, we suspect that this book will be found very helpful by the intelligent, high-toned invert; and it will certainly help other people to gain an understanding of his point of view. But what a pity it is that there is a biological necessity for such a book to be written! Only the dialectical agility of a Dr. Pangloss can produce satisfaction out of so grievous a cosmic biological error.

INFLUENCES SOLAIRES ET LUNAIRES SUR LA NAISSANCE HUMAINE.
By K. E. Krafft. *Norbert Maloine*
8 francs 5½ x 9; 50 (paper) *Paris*

A contribution to astrobiology. The author is no mere theorizer, but a hard working statistician. No small amount of statistical drudgery went into this volume. Mr. Krafft believes that influences of cosmic origin, reflected in the position of sun, moon, and stars, have a profound influence upon human biological events upon the earth. This particular essay deals with the sex ratio from that point of view. The sun plays the more important rôle in male births and the moon in female. We commend the book to the attention of statisticians.

WHAT EVERYBODY WANTS TO KNOW. *The story of sex-appeal with a complete and scientific course of exercises*

designed to build health and to give you that attraction which is the basis of love and marriage.

By Lilyan I. Malmstead. *Morning Glory Products*

$3.00 *Worcester, Mass.*

6 x 7½; 128

A system of exercises and diet which, coupled with the assiduous use of "Morning Glory" moulding cream and astringent and the wearing of the "Morning Glory Step-in Girdle," is guaranteed to produce and maintain IT. Photographs of Lilyan (herself) illustrate the treatise, and there is no denying that she is restful to the eye, though Reginald, the Office Boy, says he doesn't see why she has to have on the "Morning Glory Step-in Girdle" in *every* picture. IT, we are told, is and always has been, "sex appeal." While the book strenuously devotes itself to plain and simple instruction about how to get and hold this desirable quality, nevertheless its morals are beyond reproach. "Sex should never be dissipated by promiscuity nor put up for sale" says she.

WHY WE ARE MEN AND WOMEN *or Factors Determining Sex.*

By A. L. Benedict. *Allen Ross and Co.*

$2.50 net 5 x 7⅜; 274 *New York*

This book has been written for the general reader. A great amount of scientific, pseudo-scientific, and other rather dubious material on sex determination has gone into the making of it. No doubt some readers will feel that they are acquiring a vast amount of knowledge hitherto withheld from them, but, critically considered, it is an example of the kind of popularization of science which grieves the judicious.

BIOMETRY

FORECASTING WHEAT YIELDS FROM THE WEATHER. *Elements of an Unsolved Problem. Wheat Studies of the Food Research Institute, Vol. V, No. 1.*

Food Research Institute

$1.00 *Stanford University*

8½ x 11; 44 (paper)

A timely discussion of an important problem which up to the present has been attacked by subjective rather than objective methods. Under the following headings are presented the status of the problem and lines of attack upon this increasingly bewildering phase of agricultural economics. Preliminary considerations; weather factors in plant growth; plant reactions to weather factors; some interrelations of growth factors; methods of forecasting yields from the weather; pitfalls of correlation analyses; present results and lines of improvement; bibliography.

The conclusion is reached that the main improvement in forecasting will probably come from controlled laboratory and field experiments concerning the reaction of crops to various weather factors. Too little attention has heretofore been paid in forecasting to the plant as a reacting organism. The ultimately successful solution of the problem is only possible by the coöperation of meteorologists, agronomists, physiologists, pathologists, and entomologists, working over a period of many years with improved or modified methods in each of these lines of work.

NOMOGRAPHIE.

By M. Fréchet and H. Roullet. *Armand Colin*

9 francs (paper) *Paris*

10.25 fr. (cloth)

4½ x 6¾; 208

A useful elementary treatise on graphical computation, written by a mathematician and an engineer in collaboration. It ranges both wider and deeper than Brodetsky's comparable volume on the same subject. It is clearly and simply written.

PSYCHOLOGY AND BEHAVIOR

ANATOMY AND THE PROBLEM OF BEHAVIOUR.

By G. E. Coghill. *The Macmillan Co.*
$3.00 $5\frac{3}{8}$ x $8\frac{1}{2}$; xii + 113 *New York*

In the course of three lectures given at University College, London, the author presents his interesting and highly important work on the correlation of the structural development of the nervous system with the development of behavior. The work was chiefly upon *Amblystoma*, which in many respects is an ideal organism for such experimental studies.

Lecture I deals with the development of the behavior pattern in *Amblystoma* and the nervous mechanism which forms a basis for such a pattern. The following summary is given:

> The behavior pattern develops in a regular order of sequence of movements which is consistent with the order of development of the nervous system and its parts: in a relatively precise manner physiological processes follow the order of their embryological development in the functions of aquatic and terrestrial locomotion and feeding: behavior develops from the beginning through the progressive expansion of a perfectly integrated total pattern and the individuation within it of partial patterns which acquire various degrees of discreteness.

That the nervous mechanisms have their origin in the functions and structures of early embryonic life is the thesis of his second lecture. In the embryo, before the neural processes have appeared, there is complete integration within the tissues brought about by a coördination of the processes of growth. Many amphibia exhibit a coördination of the ectodermal cilia, causing a constant movement within the egg membrane. The paths of the nervous system are "blazed" in the early embryonic stage, the preneural pattern of localized centers determining where the differentiation of nerve cells shall occur later. The hypothesis is offered that "a gradient of electric potential acting along the external limiting membrane is the essential factor in determining the path along which the nascent nerve cell shall grow." The gap between the early non-nervous condition of the embryo where there is already perfect integration and the later stage where the nervous system appears is merely superficial. There is, in fact, an overlapping of the preneural system of integration upon the neural in the regular course of development, and this overlapping is highly significant in interpreting the development of behavior in the organism.

In the third and last lecture the author "shows how the preneural process of growth and differentiation in the nervous system, and particularly in the individual nerves, participates in the function of the nervous system as a whole."

There is a bibliography of two and a half pages, but no index. This is an important book.

CHIMPANZEE TRANSLOCATION BY MEANS OF BOXES. *Comparative Psychology Monographs Vol. 5, No. 3, Serial No. 25.*

By Harold C. Bingham.
The Johns Hopkins Press
$1.75 7 x $10\frac{1}{4}$; 91 (paper) *Baltimore*

An account of experiments in stacking boxes to reach a lure under more controlled

conditions than in the similar experiments of Yerkes and Köhler. Evidence is found of ideational behavior.

THE BATTLE OF BEHAVIORISM. *An Exposition and an Exposure.*
By John B. Watson and William MacDougall. *W. W. Norton and Co., Inc.*
$1.00 4¼ x 6½; 96 *New York*

The debate over behaviorism before the Psychological Club of Washington in 1924 is now published in Norton's "New Science Series," with a postscript by MacDougall, in which he takes the opportunity "to draw the attention of readers of this booklet to several of my more recent publications on this topic." In spite of a natural sympathy with Watson as the victim of MacDougall's forensic tricks, we cannot help doubting whether, in a world where even the electrons are coming to have a purpose, he will succeed in keeping purpose out of psychology.

THE MIND OF A GORILLA. *Part III. Memory. Comparative Psychology Monographs Vol. 5, No. 2.*
By Robert M. Yerkes. *The Johns Hopkins Press*
$1.75 7 x 10¼; 92 (paper) *Baltimore*

This is the third and final report by Professor Yerkes on his remarkably interesting series of studies on the mental and physical development of the captive female gorilla, Congo. It is most unfortunate that the experimenter could not have carried out his plan of spending some weeks each year in following her development to maturity. The death of Congo, due apparently to acidosis, secondary to ileocolitis, occurred in April, 1928. Studies made on her skeleton indicate that she was approximately eight years old. The rate of growth which different portions of the gorilla's body exhibited was exceedingly irregular. At one time the lower extremities would grow with greater rapidity—at another, the head or upper extremities. Regarding the psychobiological development and status the author states that

> The subject continued to exhibit in increasing variety, and especially in affective attitude and aspects of adaptivity, indications of transition from childhood to early maturity. Behavior suggested adolescence, but this was not definitely confirmed by physical status. Naïveté and the inhibitions due to timidity and lack of confidence gradually and increasingly gave place to such freedom and assurance of action as in human life indicate familiarity, experience, wisdom.

There was indication that experience gained in solving problems previously presented to her was transferred, in part, at least, to the solution of new problems and situations. There was lack of curiosity and desire to imitate. She never exhibited violent emotions. In sharp contrast to man and chimpanzee the investigator found Congo "slow in sensory reaction, perception, discrimination, decision, ideation (or their physiological equivalents), and in behavioral adaptation." Although there was no evidence that the menstrual periods had been established her sexual behavior and sex play indicated that she was in the adolescent stage of development and approaching sexual maturity.

THE PSYCHOLOGY OF LANGUAGE. *By Walter B. Pillsbury and Clarence L. Meader.* *D. Appleton and Co.*
$3.00 5⅛ x 10; ix + 306 *New York*

This book, by two distinguished scholars, is the logical outgrowth of the development of researches along two lines

—on the one hand, a study of psychology so far as it bears on language, and, on the other hand, a study of the origin, growth and interrelations of languages. The development of the intricate articulate movements of speech from the primitive so-called vegetative processes of the organism is traced and the relation of thought and emotion to those same physiological processes. The psychological interpretation of language based on a study of the science of phonetics and linguistics is discussed. There are many interesting sections throughout the book, among which may be mentioned the discussions of the origin and movements of articulation, the primitive forms of memory, the process of learning and the Morse Code, and the real distinction between word and sentence.

ANIMAL PSYCHOLOGY FOR BIOLOGISTS.

By J. A. Bierens de Haan.

University of London Press, Ltd.

4 s. 6 d. net $5\frac{1}{2}$ x $8\frac{1}{2}$; 80 *London*

This little book contains three lectures given at King's College, University of London. It is an interesting and stimulating presentation of a point of view regarding animal psychology which seems to us to be sound and useful. The author feels that the extreme "behaviorist" and the extreme anthropopsychic positions are equally to be condemned as philosophical guides to the actual investigation of animal psychology. He believes that higher animals (for example, dogs) have a "kind of practical intelligence, an understanding of the relations of things and an insight into the results of their actions which is sufficient for the needs of practical life." There is a bibliography covering three pages, but no index.

MODERN PROGRESS IN ZOOPSYCHOLOGY (*In Russian*).

By D. N. Kashkaroff.

Soviet Government Printing Office

3.75 roubles *Leningrad and Moscow*

$5\frac{3}{4}$ x $8\frac{3}{4}$; 425

The book represents a very thorough and critical survey of the field of modern psychology of animals, or the science called in the United States "behaviorism." The author is a great admirer of American experimental methods as applied to the study of animal psychology. In the preface he expresses the opinion that it is only thanks to these new ideas and methods that the position of zoopsychology has found its justification among other biological sciences. More than three hundred special papers are cited in the list of literature, of which nineteen only are original Russian ones. The majority of those in foreign languages belong to American authors. The book will certainly open a new period of acquaintance of Russian reading circles with the progress of exact psychology in America. So far as we know, no other European country contains such a splendid review of the brilliant modern American zoopsychological movement.

BIBLIOGRAPHY OF RESEARCH STUDIES IN EDUCATION 1926–1927. *Department of the Interior Bureau of Education Bulletin No. 22.*

By John D. Wolcott.

U. S. Government Printing Office

25 cents *Washington*

$5\frac{7}{8}$ x $9\frac{1}{4}$; vii + 162 (paper)

Lists 1540 researches in education published in the United States during the year ending June 30, 1927. An author and subject index and one of institutions are supplied.

ADAPTIVE MOTOR HABITS OF THE MACACUS RHESUS UNDER EXPERIMENTAL CONDITIONS. *A Contribution to the Problem of "Labour Processes" of Monkeys.*

By N. Kohts. Zoopsychologisches Laboratorium am Museum "Darwinianum."

7.50 rubles *Moscow*

7 x 10¾; 368 (paper)

A detailed account in Russian of an extensive experimental research on the behavior of the monkey. There is a summary in English covering 27 pages. The distinguished authoress is of the opinion that the macaque is a product of regressive evolution "down from better developed ancestors." He is, as he exists today, incapable of work, in the human sense. The volume is illustrated with 24 plates and 67 text figures. It is a contribution of first rank importance to the study of animal behavior and psychology.

THE GROUP MIND. *A Sketch of the Principles of Collective Psychology with Some Attempts to Apply Them to the Interpretation of National Life and Character.*

By William McDougall. G. P. Putnam's Sons

$3.50 5¼ x 8½; xxx + 418 *New York*

This is the second edition of McDougall's well known book. The author notes that some recent expressions of scientific thought such as that of the *Gestalt* psychologists and the Holism of General Smuts support his idea of the Group Mind as a valid scientific entity, though it is still depreciated by most psychologists. We think ourselves that the fundamental notion is less dubious than the elaboration in the text. Of his subject the author remarks: "For to the obscure questions of fact with which he deals, it is in the nature of things impossible to return answers supported by indisputable experimental proofs." Perhaps that puts as well as may be the weakness from which his conclusions suffer.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

DECIMALISM *or Progressive Selection. Aristocracy and Democracy transcribed in a fantasia of Common Sense. Offered seriously to those who when the wind is southerly know a hawk from a handsaw.*

By A Citizen of No Importance.

Richard G. Badger

$1.00 5 x 7½; 75 *Boston*

This is an interesting little tract, which is worth reading in spite of its bizarre title, and unconventional spelling. The idea of the book is the not entirely novel one that this might be a better country to live in if the method of choosing the people to run the government, local and national, were altered to something totally different from what it now is. There is a good deal of trenchant and sensible criticism in the book, and the author's panacea is not bad, on paper. But it has about as much chance of being adopted as a hawk has to become a handsaw, to change the author's pleasant alliteration.

THE TURNING POINT. *A Revised Edition.*

By Richard J. Flanagan.

Perry and Elliott Co.

5 x 7¾; 77 (paper) *Boston*

Once more our friend opposed to excess in the drinking of water comes to the fore (see QUARTERLY REVIEW OF BIOLOGY, Vol. III, p. 598). He has enlarged and, in

unimportant ways, altered his dissertation on the subject.

THOMAS HOBBES' MECHANICAL CONCEPTION OF NATURE.
By Frithiof Brandt. *Librairie Hachette*
18 shillings (paper) *London*
21 shillings (cloth)
7 x 10½; 399 (paper)

This thorough analysis of the writings of Thomas Hobbes was originally published in Danish in 1921, as the author's thesis for the doctorate. It is a service to all students of the history and philosophy of science to have this scholarly treatise available in English. The basic result is to show that it is in a real sense misleading to regard Hobbes solely as a materialist. "He is the philosopher of motion as Descartes is the philosopher of extension." Hobbes is "a philosopher of mechanism in a strict, unsurpassed sense."

OUR KNOWLEDGE OF THE EXTERNAL WORLD.
By Bertrand Russell.
W. W. Norton and Co., Inc.
$3.00 5½ x 8⅜; ix + 268 *New York*

The growing general interest in philosophy has called forth the republication of a number of really important philosophical books for popular consumption. Of current writers in English, Russell is probably the ablest in combining genuine philosophical authority with a clarity of statement intelligible to the non-professional reader. The reissue in editions of moderate cost of some of his early works by the W. W. Norton Company is therefore to be heartily welcomed. The present volume comprises the author's Lowell Lectures delivered in 1914 before the war turned Mr. Russell's attention to the consideration of problems of immediate social concern, and away from metaphysics, to the great loss, we think, of philosophy. They should be of interest to the thoughtful scientist, since they are concerned with the problem of understanding the physical world. But since the author deliberately defines the field of philosophical inquiry to exclude those particular problems which can be solved by the usual scientific procedures, the practicing investigator is not likely to get any immediate assistance. Russell attacks the intuitionist method of arriving at truth and supports an analytical procedure in philosophy as well as in physical science. For this, logic is indispensable, but the older syllogistic logic of Aristotle is inadequate, and an outline is given of the newer logistic or mathematical logic. Many of the ideas here popularly summarized have been elaborated in other later writings both by Russell and his coworker Whitehead, the latter particularly in his *Science and the Modern World.*

LEIBNIZ.
By Herbert W. Carr. *Little, Brown, and Co.*
$3.00 5½ x 8½; vi + 222 *Boston*

In this, the first of a series of monographs on the philosophers who have mainly influenced Western thought, Professor Carr, after a brief sketch of the life and intellectual milieu of Leibniz, gives a more detailed discussion of his philosophical principles and of his influence on later generations. According to Carr's interpretation Leibniz was an important precursor both of the theory of relativity and of neo-vitalism.

THE COST OF BIOLOGICAL BOOKS IN 1929

By JOHN R. MINER

Institute for Biological Research, Johns Hopkins University

AT THE end of the first volume of THE QUARTERLY REVIEW OF BIOLOGY (Vol. I, pp. 605–608, 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1929.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in earlier years.

II. *Germany.* In the number of books sent in by publishers for review, Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other Countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.*

Table 1 gives, for each of these eight rubrics, (*a*) the total number of pages in the books received for review; (*b*) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (*c*) the average price per page *in cents*.

TABLE 1

Prices of biological books, 1929

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
English-American	9,021	$171.40	1.90
Other countries	3,494	58.58	1.68
Germany	21,209	350.05	1.65
England	9,340	120.41	1.29
United States	79,710	905.39	1.14
France	11,371	53.66	0.47
British Government	392	1.54	0.39
U. S. Government	5,625	13.20	0.23

In order to facilitate comparison in respect of book prices, Table 2 has been prepared. In this table the following items are included: (*a*) the average price per page, in cents, for the years 1926–1929; (*b*) the absolute changes in average price per page, in cents, between 1926 and 1929, and between 1928 and 1929, a + sign denoting an *increase* in 1929 as compared

with the earlier years, and a — sign denoting a *decrease;* (*c*) the percentage differences of the 1929 average price per page from those of 1926 and 1928, the + sign again indicating that the books were on the average higher in price in 1929 than they were in the earlier years, and the — sign that they were lower.

The first point to be noted from Table 1 is the continued increase in the total amount of book material noticed in THE QUARTERLY REVIEW OF BIOLOGY. The total number of pages reviewed in 1929 is 140,162, an increase of 14.7 per cent over 1928, and of 69.7 per cent over 1926. The absolute increment of number of pages reviewed, which was almost constant in previous years, has decreased slightly in 1929. Apparently book material noticed is tending of its own accord towards an asymptote, but the amount of space available for book reviews may necessitate fixing a limit lower than this natural asymptote.

Turning to the prices given in Table 1 we find that the English-American books, which in 1926 and 1927 had been the most expensive but in 1928 had been slightly cheaper than the German books, again head the list. It should, however, be remembered that these prices include both transportation and the United States tariff, of 25 per cent ad valorem on books bound in leather, and of 15 per cent on those bound in other materials. For other groups the prices given refer to the country of publication and do not therefore include either of these charges.

As usual the biological books published by the United States Government stand at the bottom of the list, and next to them the British Government with one book on which the price was known. This is naturally too small a sample to be of much significance. France continues to produce the cheapest commercially published scientific books, costing on the average less than half as much as those of any other country.

As to the trends in prices shown in Table 2, England and the United States Government, which in previous years had shown a consistent decrease in price per page from year to year, in 1929 both show an increase. For English books this is large enough to bring the price slightly above the 1926 level, but the United States Government books, in spite of the increase, are still 25.8 per cent below 1926.

TABLE 2

Comparison of the prices of biological books from 1926 to 1929

ORIGIN	AVERAGE PRICE PER PAGE				CHANGE + OR — FROM 1926 TO 1929		CHANGE + OR — FROM 1928 TO 1929	
	1926	1927	1928	1929	Absolute	Relative	Absolute	Relative
	cents	*cents*	*cents*	*cents*	*cents*	*per cent*	*cents*	*per cent*
English-American	1.55	1.39	1.46	1.90	+0.35	+22.6	+0.44	+30.1
Other countries	1.51	0.78	1.13*	1.68	+0.17	+11.3	+0.55	+48.7
England	1.28	1.14	1.09	1.29	+0.01	+0.8	+0.20	+18.3
United States	1.12	1.09	1.14	1.14	+0.02	+1.8	0	0
Germany	1.09	1.20	1.48	1.65	+0.56	+51.4	+0.17	+11.5
British Government	—	0.96	1.26	0.39	−0.57†	−59.4†	−0.87	−69.0
France	0.35	0.36	0.45	0.47	+0.12	+34.3	+0.02	+4.4
U. S. Government	0.31	0.24	0.21	0.23	−0.08	−25.8	+0.02	+9.5

* With two special treatises omitted as explained in Vol. III, p. 601.

† Change from 1927 to 1929.

The German and French biological books, on the other hand, still show a steady rise in price per page. For our sample the German biological books were 11.5 per cent higher in 1929 than in 1928, and 51.4 per cent higher than in 1926. The corresponding percentage increases in the price of French biological books were 4.4 and 34.3 per cent. In the case of the French books the absolute price is so low that the percentage increase does not matter practically. For the German books, also, although they are among the highest priced on our list, there is one encouraging sign. The rate of increase in price of 1929 over 1928 is only half that of 1928 over 1927. Let us hope that German biological books are approaching a stable price level. There was no change in the price of biological books commercially published in the United States from 1928 to 1929 and only a slight increase over 1926 and 1927.

If all the books noticed in THE QUARTERLY REVIEW OF BIOLOGY in 1929, regardless of origin, are lumped together and compared with all the books noticed in earlier years it works out that the average price per page in 1926 was 1.097 cents, 1.030 cents in 1927, 1.095 cents in 1928, omitting the two very expensive books noted, and 1.194 cents in 1929. This indicates an *increase* in average price of 9.0 per cent in 1929 as compared with 1928, and of 8.8 per cent as compared with 1926. On the whole it is obvious that, in the period reviewed, no violent price changes have occurred in either direction, if one envisages a generally balanced library of current biological books.

In concluding these notes for the present year, we should like again to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only fractions of the biological works there published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of THE QUARTERLY REVIEW OF BIOLOGY regarding book prices.

INDEX

Abderhalden, E., Biological Technique, 146, 147, 266, 287, 289, 565, 571, 582, 587, 589
d'Abro, A., Evolution of Scientific Thought from Newton to Einstein, 152
Acorn storing woodpeckers, 457
Acquired characters, inheritance of, and the thyroid, 369
Activities of animals as factor in their well being, 465
Adapis, 240
Adaptiveness in food storing, 472
Adler, A., Organ Inferiority, 449
Air-sacs in insects, 222
Alexander, J., *et al.*, Colloid Chemistry, 446
Allcroft, A. H., The Circle and the Cross, 128
Allen, Bennet M. Influence of Thyroid Gland and Hypophysis on Growth and Development of Amphibian Larvae, 325–352
Allorge, P., *et al.*, Ecology of High Mountains, 565
Alpatov, W. W., Biometrical Studies on Variation and Races of the Honey Bee, 1–58.
Altenburg, E., How We Inherit, 122
American Forests and Forest Products, 142
American Negro, 575
Amphibian larvae, influence of thyroid and hypophysis on growth of, 325
Amylase of waxy and non-waxy seeds and pollen, 538
Anderson, W. K., Malarial Psychoses and Neuroses, 150
Andrews, E. A., Population of ant mounds, 248–257
Annand, P. N., Adelginae of North America, 435
"Anomaly," The Invert, 591
Ant mounds, populations of, 248
Anthony, H. E., North American Mammals, 277
Apáthy, S., on neurofibrils, 160
Apis mellifera, 1
Apis remipes, 50
Aquatic insects, respiration in, 226
Arbeláez, E. P., The Davalliaceae, 141
Aron, M., Life and Reproduction, 566
Ascoli, A., Antituberculous Vaccination, 587
Ashbrook, F. G., Fur-Farming for Profit, 138
Association of Anatomists, Proceedings, 584

von Baer, K. E., 197
Bailliart, P., Retinal Circulation, 443
Balanosphyra formiscivora, 455
Barcroft, J., Respiratory Function of the Blood, 284
Batchelor, J., Ainu Life and Lore, 430
Bateson, B., William Bateson, 120
Bateson, W., Scientific Papers, 420
Bauer, H., Halogenization, 589
Bauer, K. H., Mutation Theory of Cancer, 121
Baur, F., Correlation, 447
Baynes, E. H., Book of Dogs, 121
Bees, variation and races of, 1
Behning, A., Life of the Volga, 426
Bělář, K., Cytological Basis of Heredity, 421
Benedict, A. L., Why We Are Men and Women, 592
Benedict, F. G., Measurement of Metabolism, 587
Berkson, Joseph, The Mechanics of Teleology, 415–419
Bertalanffy, L., Morphogenesis, 265
Besredka, A., Studies on Immunity, 146
Bethe, A., on neurofibrils, 163
Bezzi, M., Diptera of the Fiji Islands, 279
Bierens de Haan, J. A., Animal Psychology, 595
Bingham, H. C., Chimpanzee Translocation by Means of Boxes, 593
Sex Development in Apes, 149
Biochemical studies on physiology of a gene, 528
Biochemistry (book reviews), 146, 286, 444, 589
Biological books, cost of in 1929, 598
differences of bee races, 43
Biometry (book reviews), 289, 447, 592
Bird malaria, 59
Boas, F., Materials for Study of Inheritance in Man, 421
Primitive Art, 567
Bodansky, M., and Fay, M. S., Physiological Chemistry, 148
Bogardus, E. S., Immigration and Race Attitudes, 433
Bois, D., Food Plants, 580
Bolton, E. R., Oils, Fats and Fatty Foods, 147
v. Bonde, C., Comparative Zoology, 578
Bose, J. C., Motor Mechanism of Plants, 439
Botany (book reviews), 140, 281, 438, 579
Bouin, P., Histology, 585
Bounhiol, J.-P., Life, 425
Bousquet, G. H., Vilfredo Pareto, 130
Bowen, Robert H., Cytology of Glandular Secretion, 299–324, 484–519
Bower, F. O., The Ferns, 438
Bowley, A. L., F. Y. Edgeworth's Contributions to Mathematical Statistics, 289
Bozler, E., on neurofibrils, 165
Brandt, F., Thomas Hobbes' Mechanical Conception of Nature, 597
Brigham, A. P., United States, 129
Brink, R. A., Physiology of a Gene, 520–543
Browne, L., Graphic Bible, 296
Buchanan, R. E., and Fulmer, E. I., Physiology and Biochemistry of Bacteria, 122
Burbridge, B., Gorilla, 151

Burlingame, L. L., *et al.*, General Biology, 266
Burnside, W., Theory of Probability, 447
Buytendijk, F., Psychology of Animals, 293

Cable, L. E., Food of Bullheads, 279
Cady, M. E., and Howell, F. A., Book of Nature, 563
Calmette, A., Bacillary Infection and Tuberculosis, 146
Cameron, J., Bureau of Biological Survey, 576
Cancer and Cancer Research, 286
Captorhinus, 238
Carassius, 92
Carnegie Institution of Washington, Contributions to Embryology, 585
Papers from Tortugas Laboratory, 576
Carpenter, K. E., Life in Inland Waters, 426
Carr, H. W., Leibniz, 597
Castellani, A., Fungi and Fungous Diseases, 588
Cattell, P., Dentition as a Measure of Maturity, 272
Caucasian bee races, 36
Celli, A., Malaria in the Roman Campagna, 587
Census of Epileptics of Surrey, 275
Chandler, W. H., North American Orchards, 281
Chappel, H. G., Jaws and Teeth of Ancient Hawaiians, 132
Chemical senses of insects, 100
Chimpanzee, 241
Chittenden, R. H., History of the Sheffield Scientific School, 295
Chondriosome, 488
Chromidia in secretion, 321
Chromosomes of fish, 96
"A Citizen of No Importance," Decimalism, 596
Clark, A. J., Comparative Physiology of the Heart, 145
Clark, W. M., Determination of Hydrogen Ions, 287
Clements, F. E., Plant Succession and Indicators, 581
Climatic factors, effect on suction force, 401
Clunn, H., An Analysis of Life, 569
Cock, R., Evolution and War, 119
Coghill, G. E., Anatomy and the Problem of Behavior, 593
Coker, W. C., and Couch, J. N., Gasteromycetes of Eastern United States and Canada, 281
Colony variation in bees, 2
Color reactions of starch with iodine, 529
Combes, R., Life of the Plant Cell, 580
Comparative psychology, 455
Conway, H. M., Livestock Review for 1927, 262
Cooper, J. F., Technique of Contraception, 148
Cori, C. I., The Nature Lover at the Sea Shore, 426
Corn-Borer Control Campaign, 136
Cost of biological books in 1929, 598
Crofts, J. M., and Jones, D. C., Secondary School Examination Statistics, 271
Cynidiognathus, 239
Cytology of glandular secretion, 299, 484

Dall, W. H., and Ochsner, W. H., Fossil Mollusca and Landshells of the Galapagos Islands, 279
Daniel, J. F., Elasmobranch Fishes, 280
Darwin, L., What is Eugenics? 435
Dashiell, J. F., Objective Psychology, 293
Davis, W. M., Coral Reef Problem, 123
Dawson, C., Age of the Gods, 432
Dawydoff, C., Comparative Embryology of Invertebrates, 142
Day, E. E., and Thomas, W., Growth of Manufactures 1899 to 1923, 429
Deaf-Mute Population of United States 1920, 128
Death of plants from low temperature, 113
De Beer, G. R., Vertebrate Zoology, 435
Defries, A., The Interpreter Geddes, 271
Degeneration theory of secretion, 304
De Kruif, P., Hunger Fighters, 274
Delabarre, E. B., Dighton Rock, 428
Dennie, C. C., Syphilis, 442
De Omnibus Rebus et Quibusdem Aliis (book reviews), 151, 294, 449, 596
Determination as chemical differentiation, 545
Development of fish, 96
Dewar, D., Birds at the Nest, 151
De Wolff, H. J., Cancer, 444
Diapea, W., Cannibal Jack, 276
Dimnet, E., Art of Thinking, 449
Distribution of California woodpecker, 460
Dixon, R. B., Building of Cultures, 133
Doflein, F., and Reichenow, E., Protozoology, 437
Donahue, A. M., Illegitimate Children, 572
Donaldson, H. H., Size of Body and Organs of Rat, 562
Dorsey, G. A., Hows and Whys of Human Behavior, 448
Dow, G. S., Society and Its Problems, 575
Draper, G., Beaumont Foundation Lectures, 568
Drew, G. A., Laboratory Manual of Invertebrate Zoology, 280
Dreyfus-Sée, G., Immunity of the Infant, 121
Dublin, L. I., Health and Wealth, 124
Duggan-Cronin, A. M., Bantu Tribes of South Africa, 276
Dugmore, A. R., African Jungle Life, 278
Dunn, L. C., Anthropometric Study of Pure and Mixed Hawaiians, 132
Dunton, W. R., Jr., Occupational Therapy, 273
Dürken, B., Experimental Zoology, 425
Dyar, H. G., Mosquitoes of the Americas, 279

Eaton, F. M., and Belden, G. O., Leaf Temperatures of Cotton, 579

Ecology, animal, 455
Eddington, A. S., Nature of the Physical World, 451
Edmondson, C. H., Ecology of an Hawaiian Coral Reef, 277
Egg, mammalian, size of, 373
Ellis, C., and Wells, A. A., Chemical Action of Ultra-Violet Rays, 589
Ellis, R. S., Psychology of Individual Differences, 293
Environment, influence on bees, 10
Eobaphetes, 237
Ergastoplasm, 485
Eusthenopteron, 234
Evaporation, effect on suction force, 410
EVOLUTION (book reviews), 118, 258, 420, 562
Ewing, H. E., Scorpions of Western United States, 135
Excretion, Ranvier's definition of, 300

FERRIS, G. F., Systematic Biology and the Mutation Theory, 389–400
Ferris, G. F., Principles of Systematic Entomology, 424
Fidlar, E., New Factors in Respiration, 586
Financial Statistics of Cities 1926, 434
Finley, W. L. and I., Wild Animal Pets, 138
Fischel, A., Human Embryology, 584
Fish, Mendelian inheritance in, 83
Fisk, E. L., and Addoms, R. M., Laboratory Manual of General Botany, 282
Flanagan, R. J., The Turning Point, 596
Fleischmann, A., Zoology, 280
Fogg, H. and N. M., Encyclopedia of Caged Birds, 421
Food Research Institute, Forecasting Wheat Yields from the Weather, 592
Food storing, 457
Formica exsectoides, 248
Foster, T. S., Travels and Settlements of Early Man, 570
Fowler, G. H., Science of the Sea, 578
Fowler, H. W., and Bean, B. A., Fishes of Families Pomacentridae, Labridae, and Callyodontidae, 136
Fréchet, M., and Roullet, H., Nomography, 592
Freud, S., Future of an Illusion, 449
Problem of Lay-Analyses, 294
Friedmann, H., The Cowbirds, 578
Fürth, O., Physiological and Pathological Chemistry, 286

Galstoff, P. S., Function of the Oyster Gills, 278
Gann, T., Discoveries and Adventures in Central America, 568
Gaskell, A., What is Life?, 422
Gates, G. S., The Modern Cat: Her Mind and Manners, 291
Gates, R. R., Cytology of *Oenothera*, 421
Gellhorn, E., Permeability, 586
Gene, physiology of, 520
GENERAL BIOLOGY (book reviews), 122, 262, 422, 565
GENETICS (book reviews), 120, 262, 420, 564
Genetics Congress, Proceedings of Fifth International, 121
Geographical variation of bees, 23, 51
Gesell, A., Infancy and Human Growth, 127
GILCHRIST, FRANCIS G., Determination of Neural Plate in Urodeles, 544–561
Gill, C. A., Genesis of Epidemics, 588
Glandular secretion, cytology of, 299, 484
Goebel, K., Organography of Plants, 580
Goldberger, J., *et al.*, Endemic Pellagra in South Carolina, 574
Golgi apparatus, 491
GOODRICH, H. B., Mendelian Inheritance in Fish, 83–99
Gould, G. M., Medical Dictionary, 296
Gould, R. T., Oddities, 450
Graham, S. A., Forest Entomology, 577
Gramet, C. A., Biology Laboratory Guide, 566
Granular nature of secretion, 305
Granule doctrine, 484
Gray, J., Ciliary Movement, 123
Greaves, J. E. and E. O., Bacteriology, 141
Gregory, J. W., Human Migration and the Future, 270
GREGORY, WILLIAM K., Palaeomorphology of Human Head, 233–247
Gregory, W. K., Our Face from Fish to Man, 562
Grey, E. C., Food of Japan, 441
Grimpe, G., and Wagler, E., Fauna of North and Baltic Seas, 437
Grinnell, J., Ornithology of Lower California, 437
Groves, E. R., and Ogburn, W. F., American Marriage and Family Relationships, 431
Growth and thyroid, 353
Gruvel, A., Fishing in Prehistory, Antiquity, and among Primitive Races, 134
Gun, W. T. J., Hereditary Ability, 434

Haire, N., More Medical Views of Birth Control, 288
Hales, B. J., Prairie Birds, 280
Hall, E. R., Outbreak of House Mice, 438
Hall, H. M., Genus *Haplopappus*, 579
Hamilton, G. V., A Research in Marriage, 590
and MacGowan, K., What is Wrong with Marriage? 590
HAMMETT, FREDERICK S., Thyroid and Growth, 353–372
Hammett, F. S., Physiology of the Thymus, 284
Hance, R. T., Radio Talks on Zoology, 140
Hankins, F. H., Introduction to the Study of Society, 268
Hanström, B., Nervous System of Invertebrates, 583

Harris, H. W., Human Merchandise, 133
HARTMAN, CARL G., How Large is the Mammalian Egg? 373–388
Hartshorne, H., and May, M. A., Studies in the Nature of Character, 428
Harvey, H. W., Biological Chemistry and Physics of Sea Water, 262
Harvey, W., *De Motu Cordis*, 284
Hatch, W. J., Land Pirates of India, 568
Hathaway, E. S., Acclimatization of Fishes and Amphibians to High Temperature, 139
Haupt, A. W., Biology, 265
Head, palaeomorphology of, 233
Heesen, W., Plankton, 266
HEGNER, ROBERT, Experimental Studies of Bird Malaria, 59–82
Hegner, R., *et al.*, Animal Parasitology, 579
Heidenhain, L., Malignant Tumors, 144
Heilborn, A., Opposite Sexes, 435
Heilbrunn, L. V., Colloid Chemistry of Protoplasm, 445
Hemicellulose in waxy and non-waxy starch, 532
Henderson, K., Prehistoric Man, 273
Henderson, L. J., Blood. A Study in General Physiology, 266, 415
Henrici, A. T., Morphologic Variation and Rate of Growth of Bacteria, 422
Henshaw, H. W., *et al.*, Book of Birds, 138
Hertz, F., Race and Civilization, 433
Hildebrand, S. F., and Schroeder, W. C., Fishes of Chesapeake Bay, 140
Hingston, R. W. G., Problems of Instinct and Intelligence, 448
Hirsch, N. D. M., East Kentucky Mountaineers, 133
Hochstetter, F., 182
Hoffman, F. L., Problems of Longevity, 573
Holloway, T. E., *et al.*, Sugar-Cane Moth Borer in United States, 137
Holocrine glands, 302
Homo sapiens, 241
Hopkins, M. D., Employment of Women at Night, 273
Hornaday, W. T., Wild Animal Interviews, 436
HUMAN BIOLOGY (book reviews), 124, 266, 426, 566
Humidity, effect on suction force, 408
Hunter, A., Creatine and Creatinine, 147
Hunter, G. W., Biology, 423
Laboratory Problems in Civic Biology, 423
Hunter, W. S., Human Behavior, 293
Hybrids, interspecific, in fish, 93
Hypophysis, influence on growth of amphibian larvae, 338

Induction in embryology, 557
Inheritance in fish, 83
Insect respiration, 213
Insects, chemical senses of, 100
Isham, M. K., Cosmos Limited, 451
Ivanow, S., Climates of the Earth and Chemical Activity of Plants, 580

Jackson, H. H. T., Long-tailed Shrews, 280
Jamieson, P., Section Cutting, 139
Jenness, D., People of the Twilight, 274
Jentzer, A., Biological Treatment of Infections with Essential Oils, 144
Jochelson, W., Archaeological Investigations in Kamchatka, 270
Johnson, W., Gilbert White, 423
Johnstone, J., Oceanography, 265
Jordan, H. J., and van der Feen, P. J., Nerve and Muscle Physiology, 587
Junod, H. A., Life of a South African Tribe, 131

Kanner, L., Folklore of the Teeth, 133
Kashkaroff, D. N., Modern Progress in Zoopsychology, 595
Keller, P., Pollens in Swiss Peat Bogs, 283
Keller, R., and Gicklhorn, J., Bioelectrostatics, 147
Kellogg, R., *et al.*, Palaeontology of Pacific Coast, 118
Kempf, G. A., Refractive Errors in Children's Eyes, 571
Kendall, E. C., Thyroxine, 590
Kent, F. R., Political Behavior, 292
Kerschner, L., 181
King, H. D., Life Processes of Rat, 562
Klarmann, E., Preparation of Organic Compounds of Metals, 589
Klein, G., Histochemistry, 446
Klimowsky, E., Sexual Type and Culture, 149
Klingelhöffer, W., Aquarium and Terrarium Technique, 266
Knibbs, G. H., Shadow of the World's Future, 426
Knibbs, S. G. C., The Savage Solomons, 568
Kohts, N., Adaptive Motor Habits of *Macacus rhesus*, 596
Kossel, A., Protamines and Histones, 286
Krafft, K. E., Solar and Lunar Influences on Human Birth, 591
Krause, G. A., New Method of Water Sterilization, 441
Kuczynski, R. R., Balance of Births and Deaths, 427

La Master, G. C., The New Genetics, 151
Lasareff, P., Ionic Theory of the Excitation of Living Tissues, 285
Lassar-Cohn, Organic Laboratory Methods, 444
Lattes, L., Individuality of the Blood, 564
Laufer, B., Giraffe in History and Art, 138
Lebistes, 84

Lee, B., Microtomist's Vade Mecum, 139
Lee, Milton O., Respiration in the Insects, 213–232
Lefas, J., Physiognomy, 434
Lenz, F., Biology of Lakes, 425
Leriche, R., and Policard, A., Normal and Pathological Physiology of Bone, 444
Li, C., Formation of the Chinese People, 271
Li, Tsi-Tung, Effect of Climatic Factors on Suction Force, 401–414
Light intensity, effect on suction force, 408
Lindau, G., Higher Fungi, 439
Lindsey, A. W., Evolution and Genetics, 563
Linville, H. J., *et al.*, General Zoology, 579
Little, M. E., and Kempton, R. T., Laboratory Manual for Comparative Anatomy, 283
Long, E. R., History of Pathology, 440
Lotsy, J. P., and Goddijn, W. A., Voyages to Judge of Bearing of Hybridization on Evolution, 420
Lubosch, W., Outlines of Scientific Anatomy, 142
Lumière, A., Life, Disease, and Death, 122
Lundborg, H., Anthropology of the Swedish Race, 275
Lusk, G., Nutrition, 444
Lutembacher, R., Arhythmias, 588

MacBride, E. W., The Idea of Memory in Biology, 264
MacCurdy, G. G., Prehistoric Man, 276
Maccurdy, J. T., Common Principles in Psychology and Physiology, 448
MacDougal, D. T., *et al.*, Hydrostatic-Pneumatic System of Trees, 583
Maladaptivity, 478
Malaria, avian, 59
Malmstead, L. I., What Everybody Wants to Know, 591
Mammalian egg, size of, 373
Mangold, E., Animal Physiology, 286
Mann, I. C., Development of the Human Eye, 283
Manson, J. S., Human Heredity, 276
Marie-Victorin, Frère, Dynamism in the Flora of Quebec, 581
Two Remarkable Epibiotes of Mingania, 581
Markey, J. F., The Symbolic Process and its Integration in Children, 290
Marriott, W. McK., Recent Advances in Chemistry in Relation to Medical Practice, 288
Marsh, C. D., *et al.*, Coyotillo as a Poisonous Plant, 145
Marshall, A. M., The Frog, 440
Martin, H., Principles of Plant Protection, 583
Martin, R., Anthropometry, 571
Mason, F., Creation by Evolution, 119
Maternal and Infant Welfare, 267
Mather, K. F., Old Mother Earth, 262
Mathews, F. S., American Wild Flowers, 581
McCollum, E. V., and Simmonds, N., Food, Nutrition and Health, 587
McDougall, W., The Group Mind, 596
McGill, N. P., Children in Agriculture, 570
Mead, M., Coming of Age in Samoa, 269
Mendelian inheritance in fish, 83
Merocrine glands, 302
Merton, H., Formation of Ameboid Cells from Dying Infusoria, 565
Metcalf, C. L., and Flint, W. P., Destructive and Useful Insects, 436
Meyer, A. W., and McCormick, L. M., Studies on Scurvy, 442
Michael, L. G., Agricultural Survey of Europe: France, 131
Mickel, C. E., Mutillid Wasps, 138
Miller, G. S., Jr., and Allen, G. M., American Bats of Genera Myotis and Pizonyx, 140
Miner, John R., Cost of Biological Books in 1929, 598–600
Minnich, Dwight Elmer, Chemical Senses of Insects, 100–112
Mitchell, P. C., Zoological Society of London, 577
Moeller, H., Statistics, 447
Molisch, H., Length of Life in Plants, 582
Morphology (book reviews), 142, 283, 440, 583
Morse, W., Applied Biochemistry, 288
Mutation theory and systematic biology, 389

Natural History of Canterbury (New Zealand), 262
Nebenkern in secretion, 321
Needham, J., Man a Machine, 275
Needham, J. G., *et al.*, Leaf-Mining Insects, 135
Nessler, C., Story of Hair, 126
Neuberg, A., Evolution of Man, 568
Neural plate, determination of in urodeles, 544
Neurofibril hypothesis, 155
Neurone theory, 156
Nickerson, G. P., The Giant Cactus, 582
Nilsson-Leissner, Gunnar, Death of Plants from Low Temperature, 113–117
Nordenskiöld, E., History of Biology, 425
Norma basalis of skull, 233
Nougaret, R. L., and Lapham, M. H., Phylloxera Infestation in California, 137
Nucleolus in secretion, 317
Nucleus, rôle of in secretion, 310
Nystrom, A. B., Dairy Cattle Breeds, 262

Oaks and woodpeckers, 459
O'Connor, J., Born That Way, 566
Olfactory pores, 103
Olliver, C. W., Magic and Witchcraft, 275

Oppenheimer, C., and Pincussen, L., Ferments, 287, 445
Ornstein, M., Rôle of Scientific Societies in 17th Century, 153
Ortenburger, A. I., Whip Snakes and Racers, 576
Oryzias, 88
Osborn, H., Leafhoppers of Ohio, 278
Osborn, H. F., Impressions of Great Naturalists, 433
Owens, C. E., Plant Pathology, 282
Oxidation-Reduction, 148

Palaeomorphology of head, 233
Papez, J. W., Comparative Neurology, 584
Parker, G. H., Neurofibril Hypothesis, 155–178
Parman, D. C., *et al.*, Blowfly Baits and Repellants, 438
Parshley, H. M., Science and Good Behavior, 432
Pattern, physiological, of urodele egg, 551
Pavlov, I. P., Conditioned Reflexes, 443
Pearse, A. S., and Hall, F. G., Homoiothermism, 442
Pende, N., Constitutional Inadequacies, 566
Periodicity in bird malaria, 70
Perrier, E., Zoology, 137
Peter, A., Aquatic Plants of German East Africa, 439
Péterfi, T., Biological Bibliography, 264
Biological Technique, 263
Pettinari, V., Ovarian Grafts, 149
Phillips, J. C., Wild Birds Introduced into North America, 120
Physiology and Pathology (book reviews), 143, 283, 440, 586
Physiology, Normal and Pathological, 143
Piaget, J., Judgment and Reasoning in the Child, 290
Pickering, J. W., Blood Plasma, 285
Pickett, D., Mortality and the Dry Law, 134
Pickett-Thomson Research Laboratories, Annals, 443
Pillsbury, W. B., and Meader, C. L., Psychology of Language, 594
Pitkin, W. B., Twilight of the American Mind, 266
Pittenger, P. S., Biologic Assays, 147
Pituitary, influence on growth of amphibian larvae, 338
Plant Pathology and Physiology in Relation to Man, 441
Plants, death of from low temperature, 113
Plasmodium, 59
Platypoecilus, 90
Pollen-tube growth, effect of waxy gene on, 524
Ponton, T. R., Nomenclature of Diseases and Operations, 588
Population size as measure of success in adaptation, 464
of ant mounds, 248
Pore plates, 103
Promorphology of urodeles, 544
Provancher, L., and Huard, V. -A., Entomology of Quebec, 577
Psychology and Behavior (book reviews), 150, 289, 448, 593
Psychology, comparative, 455

Rabaud, É., General Biology, 424
How Animals Find Their Way About, 294
Raber, O., Plant Physiology, 281
Races of bees, 1
Ramon y Cajal, S., Degeneration and Regeneration of the Nervous System, 440
Rank, O., Traumatism of Birth, 448
Rathke, H., 194
Raven, A., Motive Forces of the Mind, 293
Ready, M. M., Physical Education in City Public Schools, 569
Reagan, Franklin P., Development of the Eutherian Vena Cava, 179–212
Reinheimer, H., Evolution by Symbiosis, 261
Respiration in insects, 213
Respiratory pigments in insects, 225
Rhagiocrine type of secretion, 307
Rice, S. A., Quantitative Methods in Politics, 430
Richet, C., Impotence of Man, 453
Ritchie, A. D., Comparative Physiology of Muscular Tissue, 586
Ritter, William E., Nutritial Activities of California Woodpecker, 455–483
Rivers, T. M., *et al.*, Filterable Viruses, 143
Rivulus, 93
Robbins, W. J., *et al.*, Growth, 424
Robinson, V., Hasheesh, 444
v. Rohden, F., Constitution Study, 571
Rosendahl, C. O., and Butters, F. K., Trees and Shrubs of Minnesota, 582
Roth, L., Spinoza, 575
Russell, B., Our Knowledge of the External World, 597
Sceptical Essays, 294
Russell, F. S., and Yonge, C. M., The Seas, 264
Ruthven, A. G., *et al.*, Snakes of Michigan, 576

Sabin, F. R., 187
Sandford, K. S., and Arkell, W. J., Prehistoric Survey of Egypt, 129
Sanger, M., Motherhood in Bondage, 446
Savory, T. H., Biology of Spiders, 436
Schaffner, J. H., Flora of Ohio, 283
Scheibe, G., Photographic Photometry of Absorption Spectra, 287
Schemann, L., Race and Mental Sciences, 130
Scheminsky, F., Electron and Ion Tubes, 147
Schiff, F., Technique of Blood Grouping, 564
Schoen, M., Problem of Fermentation, 566

Schultze, M., on neurofibrils, 157
Schwartz, L., *et al.*, Studies in Physical Development and Posture, 570
Scylacops, 238
Seasonal variation in bees, 14
Secretion, cytology of, 299, 484
Secretory cycle, 308
Sensory threshold, 107
Service, J. H., Measurement of Salinity of Sea Water, 265
Sex (book reviews), 148, 288, 446, 590
Sex and the thyroid, 354
determination and differentiation, 95
Seymouria, 237
Sharpey-Schafer, E., History of the Physiological Society, 145
Shipley, A. E., Hunting under the Microscope, 123
Showalter, W. J., *et al.*, Book of Wild Flowers, 141
Shumway, W., The Frog, 136
Singer, C., From Magic to Science, 449
History of Medicine, 296
Smalian, K., Teaching of Biology, 425
Smiley, D. F., and Gould, A. G., Community Hygiene, 573
Smith, G. M., *et al.*, General Botany, 282
Snyder, L. H., Common Birds of North Carolina, 437
Sobotta, J., Atlas of Human Anatomy, 440
Sociology of woodpeckers, 462
Spencer, B., Wanderings in Wild Australia, 572
Spencer, D. A., *et al.*, Factors that Influence Wool Production, 421
Spinoza, B., Correspondence, 453
Standing Bear, L., My People the Sioux, 131
Starch grain, composition of, 531
Stark, C. G., 200
Starks, E. C., and Howard, L. D., Comparative Anatomy, 584
Statistical Abstract for the United Kingdom, 574
Steiner, E. A., Making of a Great Race, 574
Stephenson, T. A., British Sea Anemones, 276
Stieglitz, J., *et al.*, Chemistry in Medicine, 445
Stiles, C. W., and Hassall, A., Key-Catalogue of Insects of Importance in Public Health, 135
Stiles, P. G., Human Physiology, 286
Stitt, E. R., Bacteriology, Blood Work and Animal Parasitology, 146
Stocker, O., Water Regulation of Egyptian Desert and Salt Plants, 140
Storing of food, 457
Study of Rehabilitated Persons, 431
Suction force, effect of climatic factors on, 401
Sullivan, L. R., Hawaiian Somatology, 132
Svedberg, T., Colloid Chemistry, 288
Swanson, C. O., Wheat Flour and Diet, 586
Systematic biology and the mutation theory, 389

Tanner, F. W., Bacteriology, 439
Practical Bacteriology, 439
Tao, L. K., Livelihood in Peking, 433
Taxonomy of bee races, 47
Taylor, H. O., Human Values and Verities, 125
Taylor, W. S., Morton Prince and Abnormal Psychology, 150
Temperature, effect on suction force, 406
low, death of plants from, 113
Terroine, E. F., and Colin, H., Biological Constants, 446
Theobald, Bishop, Physiologus, 280
Thermal gradients, 554
Thienemann, A., Oxygen in Lakes, 426
Thomas, J., Bon Vivant's Companion, 452
Thompson, C. J. S., Mysteries of History, 432
Thomson, J. J., Beyond the Electron, 451
Thylacinus, 240
Thyroid and growth, 353
influence on growth of amphibian larvae, 325
Torrance, A., Tracking Down the Enemies of Man, 587
Townsend, C. H., The Public Aquarium, 565
Triturus torosus, 554
Troland, L. T., Fundamentals of Human Motivation, 292
Trypanosomiasis, 443

von Uexküll, J., Theoretical Biology, 266
The Unconscious, 150
Urodeles, determination of neural plate in, 544
Usilton, L. J., and Edson, N. W., Sex Education in Senior High Schools, 447
Utterback, W. O., The Great Life Cycle, 258

Vacuome, 510
Variation of bees, 1
Vavilov, N. I., and Bukinich, D. D., Agricultural Afghanistan, 582
Vena cava, development of, 179
Verain, M., and Chaumette, J., pH in Biology, 446
Vernon, H. M., Alcohol Problem, 432
Visher, S. S., Geography of American Notables, 429
Visscher, J. P., Fouling of Ships' Bottoms, 134
Vital Statistics of Switzerland, 434
Voronoff, S., Conquest of Life, 288
Vosmaer, G. C. J., Bibliography of Sponges, 277
Voûte, A. D., Dutch Planarians, 577

Waldschmidt-Leitz, E., Enzyme Action and Properties, 590
Walker, B., Land Snails of Alabama, 576
Walsh, W. S., The Inferiority Feeling, 449
Watson, A. McL., Histology, 142

Watson, D. M. S., Palaeontology and the Evolution of Man, 420
Watson, J. B., and MacDougall, W., The Battle of Behaviorism, 594
Waxy gene in maize, 522
Weigelt, J., Recent Vertebrate Remains and Their Palaeobiological Significance, 563
Weiss, F., *et al.*, Fusarium Rot in Potatoes, 282
and Brierley, P., Spread and Repression in Potato Wart, 141
Weissenberg, R., Human Embryology, 584
Wellhouse, W. H., and Hendrickson, G., Biology, 426
Wheeler, W. M., The Social Insects, 264
White, F. W., Posterity in the Light of Science, Philanthropy and Population, 573
Wickersham, J., Bibliography of Alaska, 434
Wiggam, A. E., Exploring Your Mind, 289
Wiggers, C. J., Pressure Pulses in Cardiovascular System, 444
Wilkins, G. H., Undiscovered Australia, 569
Williams, F. X., Tropical Wasps, 139
Willis, H. S., Laboratory Diagnosis and Experimental Methods in Tuberculosis, 283
Wilson, G. L., Hidatsa Eagle Trapping, 274
Wilson, M. C., Extension Methods and Their Relative Effectiveness, 574
Wingfield, A. H., Twins and Orphans, 120
Winterstein, H., Causality and Vitalism, 123
Wolcott, J. D., Bibliography of Research Studies in Education, 595
Woodpecker, nutritial activities of, 455
Woods, E. A., Sociology of Life Insurance, 272
Work-growth ratio, 366

Yerkes, R. M., The Mind of a Gorilla, 594

Zea mays, 522
Zinsser, H., Bacteriology, 285
Zoethout, W. D., Laboratory Experiments in Physiology, 285
Physiology, 286
Zoology (book reviews), 134, 276, 435, 576